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THE UNIVERSITY OF ALBERTA

RECRUITMENT OF YOUNG IN A DECLINING POPULATION OF BLUE GROUSE

by

© JAMES EDWARD HINES

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled RECRUITMENT OF YOUNG IN A DECLINING POPULATION OF BLUE GROUSE submitted by JAMES EDWARD HINES in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

Animal populations do not grow indefinitely and recruitment, the process whereby new animals are added to the breeding population, is potentially important in determining animal numbers. Hypothetically, the "surplus" of young produced in populations of blue grouse (*Dendragapus obscurus*) might be eliminated by (1) mortality over winter, or (2) spacing behavior in spring. On Hardwicke Island, British Columbia, Canada, these hypotheses were tested from 1979-1983 on a declining population of blue grouse through radio-tracking 293 juveniles and observing color-banded birds. A second objective was to investigate the ecology of blue grouse in autumn and winter as little is know about events at this time of year that might influence avian populations.

Survival of young blue grouse over winter was not adequate to maintain a stable population, indicating that high over-winter mortality caused the population to decline. The proportion of yearling females that nested varied inversely with population density, suggesting that spacing behavior prevented some females from breeding when numbers were high. Behavior did not appear to limit numbers when population densities were relatively low as most females nested under these conditions. Number of recruits was correlated with number of young produced the previous year; therefore production likely influenced recruitment. The latter result was not consistent with either the spacing behavior or over-winter mortality hypotheses.

Fall migration was not highly synchronized among individuals and was spread over several months. Juveniles moved 0 to 15.0 km to winter range (median = 1.9 km for males and 2.3 km for females) whereas older grouse moved distances of 0 to 5.4 km with the median varying from 0.3 to 0.7 km for different sex and age classes. Juveniles, especially those moving >5 km, tended to migrate eastward from the 465-ha main study area in fall and then move westward in spring. There was little directionality in the overall pattern of migration for older grouse. Blue grouse wintered in a wide variety of successional stages (all dominated by western hemlock, *Tsuga heterophylla*) ranging from recently-logged areas to mature coniferous forest. Preferred habitats were mature forests at higher elevations (>300 m) situated close to breeding range. Needles of western hemlock and Douglas-fir (*Pseudotsuga menziesii*) comprised much of the winter diet.

Broods apparently disbanded before migration. About half of the grouse observed in winter were in flocks (usually of 2 or 3 birds) with grouse associating most frequently with individuals of their own sex and age. The median daily movement was 69 m and home ranges averaged 16.8 ± SE 2.3 ha in winter.

Natal dispersal was influenced by a complex of variables including fall migration, spring migration, and spring movements on breeding range. Long-distance dispersal occurred most frequently when grouse migrated long distances in fall but only short distances in spring. Median dispersal distance was 0.9 km for males (range = 0.2 to 2.6 km) and 1.4 km for females (range = 0.3 to 11.0 km). Dispersal distances did not vary greatly among years or with changes in population density. There was no observable influence of dispersal on survival or reproductive success.

Young females were more mobile than adult females early in spring and home ranges overlapped considerably on breeding range. Although females usually were solitary in spring, I found no evidence that they spaced themselves or their nest-sites in a regular pattern.

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1. INTRODUCTION

Animal populations vary in size from year to year because of changes in rates of birth, death, immigration, and emigration. In addition, the breeding population can be further reduced below the size set by the above factors if some animals do not breed. Biologists have been impressed by the relative stability of some animal populations (Lack 1954) and describe the process that brings about this stability as population regulation. Regulation, in the sense used by many observers, implies that the population is fairly stable and influenced by density-dependent factors. Despite widespread acceptance among ecologists, population regulation has seldom been shown to occur (Lack 1966, Moss et al. 1982) -- a fact that might be attributed to a shortage of adequate information rather than the actual absence of regulation (Lack 1966). Because it is difficult to study regulation, a useful approach to the study of population dynamics is to look for the factors that determine or limit[1] the population at any given time.

Two major, and opposing, viewpoints concerning the limitation of avian populations have been presented by Wynne-Edwards (1962) and Lack (1954, 1966). Wynne-Edwards emphasized the role of social behavior in limiting population growth and suggested that numbers seldom reached a level where resources such as food came into short supply. In contrast, Lack maintained that over-winter mortality, especially as influenced by food shortage, was instrumental in checking population growth. Other biologists, while agreeing with Lack that mortality prior to the breeding season determined the size of the subsequent breeding population, viewed predation as the most important cause of losses (Rusch and Keith 1971, Keith et al. 1977). Both Lack and Wynne-Edwards recognized that birds produced far more offspring annually than were needed to replace dying adults and felt that whatever determined number of young entering the subsequent breeding population, effectively determined population growth.

---

[1] The term *limit* describes the effect of the process that restricts population growth (Watson and Moss 1970, Moss et al. 1982). Whether such processes are acting in a regulatory manner can only be determined through long-term studies and field experiments which show that the effects are strongly density-dependent.

Several studies of mammals and birds support the view that recruitment, the process whereby young animals are added to the population, is instrumental in determining population size (see Tanner 1966, and Bendell 1972, for references). These investigations suggest that adult mortality is relatively constant from year to year and that there is an autumn to spring bottleneck, acting particularly on young animals, that restricts population increase. Unfortunately, comparatively little research has been carried out on young animals as they are difficult to find or observe throughout much of the year. Earlier work on grouse (Bendell 1972, Keppie 1979) and other birds (Lack 1966, Fretwell 1972) implicated losses of young between autumn and spring in population change and Bendell (1972) noted there was a particular need for studies during this critical period. The causes of over-winter losses are not well understood but food shortage (Lack 1966, McGowan 1969, Newton 1980), predation (Gullion and Marshall 1968, Rusch and Keith 1971), and dispersal (Keppie 1979, Watson and Moss 1979) are 3 possibilities. Dispersal is thought to play an important role in the population dynamics of birds and mammals (Krebs and Myers 1974, Anderson 1980, Gaines and McClenaghan 1980, Tamarin 1980, Watson and Moss 1979, Moss et al. 1982, Stenseth 1983) and its influence on populations of grouse particularly deserves further investigation. Watson and Moss (1979) hypothesized that socially-induced dispersal or over-winter mortality might cause cyclic fluctuations in numbers of grouse, and Keppie (1979) and Watson et al. (1984) concluded that spring dispersal was important in determining population size in spruce grouse (*Dendragapus canadensis*) and red grouse (*Lagopus lagopus scoticus*), respectively. Despite the frequent implication that dispersal plays an important role in limitation of populations, surprisingly little is known about the causes of dispersal or the eventual fates of dispersing animals.

Populations of blue grouse (*Dendragapus obscurus*) conform to the above generalization of recruitment affecting population change; numbers of breeders apparently vary in relation to the number of yearlings that enter the breeding population in spring (Zwickel et al. 1983). Mortality rates of adult grouse are relatively constant from year to year and populations rise or fall when the number of yearling recruits is either greater or smaller than the number of adults that die. In order to understand the mechanism of population limitation in this species, one must identify factors determining recruitment of yearlings.

The existence of "surplus" or "floater" individuals that do not breed is important evidence that populations are limited by social behavior (Watson and Moss 1970). In experimental attempts to find out if surplus yearlings were present in populations of blue grouse, resident grouse were removed from breeding range on Vancouver Island (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972, 1980). A general conclusion from these investigations was that more yearlings were present on removal plots than were needed to replace adult losses in either increasing or decreasing populations. Thus, the number of young surviving over winter was large enough to replace dying adults and the number of juveniles produced in one year did not seem to directly determine the size of the breeding population in the following spring (Zwickel et al. 1983). The presence of non-breeding yearlings supported the view that blue grouse populations were regulated intrinsically by spacing behavior.

In contrast to the removal studies, which had indicated large numbers of non-breeding yearlings in spring, Sopuck (1979) marked yearling grouse with radio transmitters and found that most females nested and that most males localized (a possible indication of recruitment). Hannon et al. (1982) compared the spring movements of adult and yearling females and concluded that the aggressive behavior of adults might delay nesting in some yearlings. Although most yearling females began laying a week or more later than adults, about 90% of the young grouse eventually nested which suggests that the surplus of non-breeders was small (Sopuck 1979). Sopuck (1979) gave 2 possible explanations for the seemingly contradictory results of the removal and radio-tracking studies: (1) research on radio-marked grouse followed 2 years of low production of young and perhaps a smaller than normal surplus existed those springs; and (2) recruiting yearlings may have been easier to find, capture, and equip with radios than were surplus individuals -- the sample of radio-marked grouse might not have reflected the actual abundance of non-breeders. A third explanation might also be considered: yearlings were very mobile and many grouse, identified as surplus individuals on removal plots, may have settled elsewhere had there been no removal experiment. Perhaps removal experiments exaggerated the size of the surplus.

1.1 The Present Study

Another approach to the study of recruitment is to equip young grouse with radio transmitters and follow them to their eventual fates. Hopefully, in this manner, radio-marked juveniles are "randomly" chosen from the autumn population and both "surplus" and "non-surplus" individuals are represented in the sample in proportion to their actual abundance.

Accordingly, in late summer and early autumn 1979 through 1982, 293 juvenile blue grouse were equipped with radio transmitters. My objective was to follow these grouse throughout fall and winter to document losses of young from the population and identify surplus and recruiting individuals. Two main hypotheses were tested:

Hypothesis 1: the number of recruits is determined by over-winter mortality (Lack 1966);

Hypothesis 2: the number of recruits is determined by spacing behavior in spring (Wynne-Edwards 1962).

If over-winter mortality limited numbers, I expected to find that most surviving females would nest in spring and that most males would localize on small home ranges. If behavior limited density, I expected to find surplus animals which were forced to disperse or defer breeding.

As noted by Bendell (1972) and others, our understanding of the life history and ecology of grouse in the non-breeding season is inadequate and such data are essential to our understanding of the population dynamics of the Tetraoninae and other birds. Thus, a second objective of my study was to investigate habitat use, social groupings, and movements during fall and winter. The results are presented in a series of individual manuscripts.

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2. MIGRATION IN A POPULATION OF BLUE GROUSE

2.1 Introduction

Migration, here defined as a seasonal movement between summer and winter ranges, allows individuals to use suitable breeding and wintering areas that are spatially isolated. It comes about especially when seasonal changes in the environment make an area useful for breeding but not for wintering and vice-versa.

In the foothills and mountains of western North America, blue grouse (*Dendragapus obscurus*) migrate between open breeding areas, usually at lower elevations, and montane woodlands where they spend the winter (Anthony 1903, Marshall 1946, Wing 1947, Bendell 1955, Zwickel et al. 1968). These movements have not been well documented although reports by Boag (1966), Bendell and Elliott (1967), Zwickel et al. (1968), and Sopuck (1979) suggest that distances traveled are sometimes considerable (ranging between 16 and 50 km for different areas) and that populations originating from a small area of breeding habitat spread out over a much broader area in winter.

Migration has been reported for several other North American tetraonines including spruce grouse (*Dendragapus canadensis*), sage grouse (*Centrocercus urophasianus*), and 3 species of ptarmigan (*Lagopus* spp.) (Dalke et al. 1963, Weeden 1964, Hoffman and Braun 1975, Herzog and Keppie 1980, and others). Similar movements between winter and summer ranges have been documented for other galliforms including ring-necked pheasants (*Phasianus colchicus*) and gray partridges (*Perdix perdix*) although they have not been termed migrations by the authors (Gates and Hale 1974, Weigand 1980). Most species of galliforms for which adequate data have been gathered show an apparent sex bias in distance traveled, with females moving farther, on average, than males. Similar occurrences are well known for song birds and hypotheses which might explain the phenomenon have been discussed by Ketterson and Nolan (1979, 1983), Myers (1981), and others.

Essentially, three main single-factor hypotheses have been proposed to explain differential migration of the sexes (Myers 1981, Ketterson and Nolan 1983). The *body size hypothesis* suggests that larger-bodied animals (males in most species) have a greater tolerance to cold and are better able to survive over winter at higher latitudes than are smaller-bodied individuals (usually females). Sex or age classes with smaller bodies are more apt to migrate further south to avoid the rigors of winter weather. According to the *dominance hypothesis*, members of certain sex and age classes are dominant and force subordinate animals to migrate longer distances and settle in habitats that are farther from the breeding grounds. The *arrival time hypothesis* implies that competition for resources on the breeding grounds differs among sex and age classes and one class benefits more than others from early arrival on breeding range. This sex-age class should winter as close to the breeding grounds as possible to expedite return in spring. In addition, Baker (1978) proposed a multifactorial or threshold model of migration that accommodated all of the unifactorial hypotheses (reviewed by Ketterson and Nolan 1983). Baker (1978) suggested that migration should occur when the advantages of moving outweigh the advantages of staying in one location on a year-round basis. No one explanation of differential migration seems conclusive at present although investigations supporting each hypothesis have been reported.

From 1979 to 1982, I studied the fall and spring movements of blue grouse on Hardwicke Island, British Columbia. I looked for sex-age differences in timing and distance of migration and factors that might influence formation of such patterns by observing radio-marked and color-banded individuals. In this report the fall and spring migrations of blue grouse are described and then compared to patterns of migration found in other galliforms and birds in general.

2.2 Study Area and Methods

The study area, Hardwicke Island[2] (50° 28' N, 125° 50' W), is situated in the western hemlock (*Tsuga heterophylla*) biogeoclimatic zone of British Columbia, Canada (Krajina 1965). Much of the 77 km² island has been logged since the early 1900's and the vegetation is a patchwork of successional stages ranging from newly-logged to greater than 250 years in age. Blue grouse mainly use early seral stages for breeding and a variety of successional stages in winter. The main study area for blue grouse research was 465 ha in area and consists primarily of plant communities less than 15 years in age. This is the largest continuous block of early seral vegetation on the island.

Field work was conducted on a year round basis from May 1979 to August 1982 (with the exception of January through March 1981). General methods of finding, capturing, and marking blue grouse have been described by Zwickel and Bendell (1967*a*) and Zwickel (1982). In late summer and early fall, 235 large juveniles (>8 weeks in age) were equipped with radio transmitters. Radio packages were applied as described by Brander (1968) and weighed 25 to 31 g (2 to 6% of the body weight of juveniles at this time). During winter and early spring, 10 yearling and adult males were equipped with transmitters, mainly as part of other studies (Jamieson and Zwickel 1983*a*, Lewis 1984). Radio-marked grouse were located during fall and winter to determine movements, home ranges, date of migration, and survival. Date of migration was the mid-point between the last day a grouse was found on its summer home range and the date it was next located. Survival (in days) was the period lasting from 1 September until the date a grouse was last seen alive. In addition to radio-tracking, I used a pointing dog to locate grouse on winter range. When a marked grouse was encountered, I attempted to identify it by its colored leg-bands; if it was unmarked, I attempted to capture it with a noosing pole (Zwickel and Bendell 1967*b*) and band it. Most radio-marked grouse (>95%) were initially captured on the main study area.

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[2] Appendix 2 of the thesis includes a map showing the location of Hardwicke Island.

Migration distances were calculated using the mean latitude and longitude coordinates for summer and winter observations. Fall migration distance referred to the distance from the summer to the winter home range of an individual. Spring migration distance was the distance from winter to summer home range. Directions of migration for both fall and spring were estimated using mean latitude and longitude coordinates. Directions and distances of migration for a few grouse located by dog were based on only one location during winter. This was thought to be valid because grouse were quite sedentary at this time of year (Hines 1986).

Most statistical methods follow Conover (1980) and Sokal and Rohlf (1981). Means (± SE) were used to describe central tendency in samples that were normally distributed (as determined by the Kolmogorov-Smirnoff test for goodness-of-fit) and medians and ranges are used to describe data that are not normally distributed. Such data were first normalized by log transformation if parametric tests were to be used. Directions of migration are analysed with circular statistics described by Batschelet (1981).

For comparative purposes, grouse of 3 different age classes were recognized: (1) juveniles - grouse making their first fall or spring migration, (2) yearlings - grouse making their second fall or spring migration, and (3) adults - all older grouse.

2.3 Results

Data on migration of blue grouse came from 2 sources: radio-marked and non-radioed, color-banded individuals. Grouse that were only color-banded were difficult to find and identify in winter because many individuals moved off the main study area into forested areas where they spent much of their time in coniferous trees. The sample of banded grouse observed in winter was potentially biased towards birds that moved only short distances and remained in open areas where they were easier to find and identify. In contrast, radio-marked birds could be found in all habitats and were thought to provide an unbiased sample of migration distances.

Radio-marked and non-radioed grouse were compared to determine whether the sample of non-radioed grouse provided a biased estimate of migration distances for any sex-age class (Table 2.1). This analysis revealed no significant differences between radio and non-radio groups for either adults or yearlings. However, migration distances of radio-marked juveniles were significantly greater than those of non-radioed juveniles. Thus, migration distances for adults and yearlings were based on pooled samples of radio-marked and non-radio individuals whereas distances for juveniles were based on the sample of radio-marked grouse only.

2.3.1 Fall Migration Distance

Fall movements varied greatly among individuals; some juveniles remained on or near their summer home range whereas a few moved 10 km or more to winter range (Figure 2.1). Over 3 years of study, 7 juveniles (3 males and 4 females) were known to leave the island in fall. Although migration distances for these grouse are approximate, they are included in the analyses.

To determine if migration distances of juveniles varied between sexes or years of study, data were normalized by log transformation and analysed with a 2-way ANOVA. This test revealed that migration distances did not differ between sexes ($P = 0.91$) and probably not among years ($P = 0.10$, Table 2.2).

Migration distances for the different sex-age classes were also compared with a 2-way ANOVA (Table 2.3). Distances varied greatly among age classes ($P < 0.01$) but not between sexes ($P = 0.40$) and it seemed appropriate to compare the 3 age classes only (with data for both sexes pooled). Individual comparisons (Student-Newman-Keuls test) showed that adults and yearlings did not differ in migration distance ($P > 0.05$) but juveniles differed from both adults ($P < 0.01$) and yearlings ($P < 0.01$). Fall migration distances of adults and yearlings are shown in Figure 2.2.

2.3.2 Comparison of Fall and Spring Migration Distances

Over-winter mortality of young grouse was high and, as a result, distances of spring migration were available for only 50 juveniles. The median spring distance of 1.2 km (range = 0.1 - 15.0 km) was similar to the median fall distance of 1.8 km (range = 0.3 - 15.0 km) for these 50 individuals (Mann-Whitney U-test, $P = 0.13$).

In spring of their first year of life, blue grouse search for a place to settle and breed. On Hardwicke Island, many grouse that wintered in a habitat that was unsuitable for breeding, undertook return migrations that brought them back near their place of hatch. Consequently, fall migration distances and spring migration distances were highly correlated (Figure 2.3). This was possibly an artifact of the vegetational characteristics of Hardwicke Island as much of the recently-logged area (preferred as breeding habitat) was centered around the main study area where most juveniles were radio-marked. If suitable breeding habitat had been more abundant elsewhere on the island, a different pattern of spring migration might have occurred. Despite this possibility, I do not consider the high rate of return exhibited by juveniles on Hardwicke Island to be abnormal. High rates of return have been reported for juvenile blue grouse on Vancouver Island (Jamieson and Zwickel 1983*b*, Zwickel 1983) and I believe that such migrations also would be expected under primeval conditions when suitable open breeding habitat likely occurred as small openings in mature forest.

2.3.3 Timing of Migration

The date of fall migration was estimated for 85 juveniles (Figure 2.4). Fall migration of juveniles was not a highly synchronized mass movement but rather a gradual process spread over 2 months or more (Table 2.4). Potentially, date of migration might be influenced by several variables including sex, date of hatch, and annual differences in factors such as weather or habitat conditions. I evaluated the relative effect of each of these variables on date of migration with a 2-way analysis of covariance using sex and age as fixed factors and date of hatch as a covariate. Neither *hatch date* ($P = 0.43$) nor *sex* ($P = 0.35$) seemed to have much influence on time of departure whereas *year* had a significant effect ($P = 0.01$). Annual differences in time of migration are indicated in Table 2.4.

Age of juveniles at time of fall migration varied between 65 and 155 days and averaged 114 ± 2 days ($N = 85$). A 2-way ANOVA indicated that age at departure was not dependent on sex ($P = 0.80$) but possibly was influenced by year ($P = 0.06$).

Juveniles that left breeding range early in fall were more apt to travel long distances than those that departed later (Figure 2.5). The underlying cause of this relationship is not known although it is possible that there are behavioral differences between long-distance and short-distance migrants. For example, social interactions among juveniles or between juveniles and brood females on breeding range could cause subordinate grouse to leave earlier and move longer distances (Gauthereaux 1978). This seems unlikely for blue grouse because there is little overt aggression among birds at the time of migration. Another possibility is that long-distance migrants leave breeding range before brood break-up and travel with their mothers to winter range whereas short-distance migrants move after brood break-up as hypothesized by Schroeder (1985). The areas where 46 radio-marked juveniles were sighted ≤5 days before migration were thoroughly searched with a pointing dog to find if young grouse were still in broods. Only 8 juveniles were with adult females. Further, I found no instances where juveniles wintered with their mothers and it seemed unlikely that many females were leading their young to distant winter ranges. A third possibility is that young grouse have an inherent potential to move either long or short distances (see Greenwood et al. 1979) but this could not be evaluated.

Although sample sizes for dates of fall migration of adults and yearlings were very small, trends in the data were distinct. Six radio-marked females left breeding range between 10 August and 6 October ($\bar{X}$ = 3 Sep ± SE 9 d) with the 4 non-breeding females departing before 10 September and the 2 females that raised broods departing about 15 September and 6 October, respectively. Similarly, broodless females depart for winter range before brood females on Vancouver Island (Sopuck 1979).

Comparatively few adult or yearling males were observed on breeding range in late summer indicating that members of these sex-age classes had migrated before females of the same age. Eight radio-marked adult males, followed by

Lewis (1984:38), abandoned territories between 17 June and 11 August in 1981 and moved to winter range ($\bar{X}$ = 7 July ± SE 6 d).

Spring migration followed a similar progression with older (i.e., adult and yearling) male grouse first to arrive on breeding range. Newly-arriving males were observed in the last week of February and the first week of March in both 1980 and 1982 but older females did not arrive until the first week of April in both years. Six radio-marked juvenile males arrived between 15 March and 16 April ($\bar{X}$ = 4 April ± SE 4 d). Dates of arrival for 8 radio-marked juvenile females were between 10 and 23 April ($\bar{X}$ = 16 April ± SE 14 d). These data are based mainly on long-distance migrants as time of migration was difficult to ascertain for grouse that moved only short distances.

2.3.4 Direction of Migration

Directions of fall migration did not differ from those expected by chance for samples of adult males, yearling males, adult females, yearling females, or all adults and yearlings combined (Figure 2.2, Table 2.5).

In contrast to older grouse, many juveniles moved eastward from the study area in fall (Figure 2.1, Table 2.5). Much of the directionality in the pattern of fall migration could be attributed to juveniles that moved longer distances -- when only grouse moving ≤ 5 km were considered, the pattern became essentially random. There was, however, a strong element of directionality to the pattern of migration when only grouse moving >5 km were considered. Mean angles of fall migration for juvenile males (108 ± angular deviation 68°) and juvenile females (80 ± 70°) were similar (Kuiper's 2-sample test, $P > 0.10$) and the overall mean angle for both males and females was essentially eastward (89 ± 70°).

Mean directions of spring migration did not differ from random for samples of juvenile males (143 ± 76°, $r = 0.12$, $N = 19$, $P > 0.10$), juvenile females (265 ± 71°, $r = 0.23$, $N = 31$, $P > 0.10$), or both males and females pooled (247 ± 76°, $r = 0.12$, $N = 50$, $P > 0.10$). If juveniles moving ≤ 5 km and those moving >5 km are considered separately, a different pattern emerges. Grouse moving >5 km showed a strong tendency to move westward (mean direction = 272 ± 39°, $r = 0.94$, $N = 9$, $P < 0.01$) whereas those moving ≤ 5 km showed no distinct pattern (155 ± 78°, $r = 0.03$, $N = 41$, $P > 0.10$).

2.3.5 Fidelity to Winter Ranges

Many grouse returned to wintering areas they had used in previous years. Seven adults and yearlings, observed in consecutive winters, were found within 200 m of their previous wintering sites. Ten of 13 grouse observed on winter range as juveniles and again as yearlings, wintered at the same site in consecutive years. The 3 that changed locations in their second winter had previously migrated 1.5 km or more in both fall and spring of their first year but after settling on breeding range became essentially non-migratory. Some young grouse, after migrating in fall, wintered in areas that were suitable for breeding and did not migrate far in spring. Five of 13 grouse, seen in both their first and second winters, behaved in this manner and became essentially non-migratory. Three grouse shortened migration distances as yearlings (as discussed previously) and the remaining 5 were migratory as yearlings. The shortening of migration distances by young grouse likely helped bring about the shorter migration distances typical of older age classes.

2.3.6 Differential Survival of Long- and Short-distance Migrants

Migration may have costs as well as benefits and it was my impression that juveniles migrating long-distances did not survive as well as short-distance migrants. If values greater than the median fall migration distance are considered "long" and values less than the median are considered "short", the possible effects of migration distance on survival can be evaluated (Table 2.6). For males, the survival rate of short-distance migrants significantly exceeded that of long-distance migrants and a similar analysis for females revealed a possible difference in survival rates of short-distance and long-distance migrants.

Although the data suggested that long-distance migrants did not fare as well as short-distance migrants, the data were potentially biased. On average, long-distance migrants left the study area earlier than short-distance migrants. Mortality of juvenile grouse was high in early fall and it is possible that many of the grouse that died on the study area would have become short-distance migrants had they survived (most of the long-distance migrants having already departed). To separate the relative effects of date of migration and migration distance on survival, I used multiple regression analysis with survival in days as the dependent variable and date and distance as independent variables. This analysis, conducted on a sample of 76 grouse for which all the necessary data were available, indicated that both date ($r = 0.32$, $P < 0.01$) and distance ($r = -0.25$, $P = 0.03$) were highly correlated with survival as well as with each other ($r = -0.55$, $P < 0.01$). Date was the only variable included in a multiple regression equation indicating that the correlation between distance and survival was likely a spurious one caused by the high correlation of distance and time of migration. I conclude that the difference in survival of long- and short-distance migrants was mainly an artifact of time of migration rather than an effect of distance moved, and that survival of long-distance migrants was not atypical of that of the entire population of juveniles.

2.4 Discussion

Studies of blue grouse in other areas suggested that members of the same local population tended to migrate in the same general direction (Zwickel et al. 1968, Sopuck 1979). Such directionality is likely influenced by the location of suitable wintering areas but could be influenced by geographical features such as mountain ranges and bodies of water which restrict the direction in which a grouse easily might move. For Hardwicke Island, only the sample of juveniles moving longer distances showed a strongly directional pattern in migration; juveniles moving shorter distances and adults (most of which moved shorter distances) did not. The high degree of directionality shown by long-distance migrants was likely influenced by the shape of Hardwicke Island as the only way a grouse could move a long distance was by going eastward from the main study area.

In any given year, there was great variability among individual juveniles in both date of migration and age at migration in fall. Despite this, there also were significant annual differences in both date of fall migration and age of juveniles at time of migration. Data were not sufficient to evaluate the causes of annual variations but it is possible that weather or habitat conditions were involved.

In fall, adults and yearlings of both sexes migrated shorter distances on average than juveniles, and most older grouse preceded juveniles in time of departure from breeding range. Juvenile males and females did not differ in timing or distance of migration. In spring, adult males arrived earliest on breeding range and were followed, about one month later, by young males and adult females. Juvenile females arrived latest -- about 6 weeks after adult males and 10 to 15 days after adult females and juvenile males.

At least 3 factors may have been involved in the shortening of migration distances that occurred between the first and second years of life. First, some juveniles moved long distances in fall and remained near their wintering sites in spring. Essentially, such grouse became non-migratory in subsequent years. Other grouse moved long distances in fall and spring of their first year but wintered closer to breeding range in their second year. Third, long-distance migrants may have suffered higher mortality than short-distance migrants (although the relationship between migration distance and survival was not entirely clear).

Migration may be more typical of the Tetraoninae than previously supposed, having been reported for 6 of 9 species of North American grouse (Table 2.7) and suggested, but not well documented, for 2 others (Hamerstrom and Hamerstrom 1949, 1951). Most species show sex or age differences in distance of migration. Although information concerning influences of age on migration distance is not available for all species, 2 general trends are apparent: 1) adults tend to move shorter distances than do young, and 2) males tend to move shorter distances than females. Studies of spruce grouse (Herzog and Keppie 1980), white-tailed ptarmigan (*Lagopus leucurus*) (Hoffmann and Braun 1975), willow ptarmigan (*Lagopus lagopus*) (Irving et al. 1967), and blue grouse (Bendell and Elliott 1967, this study) indicate that males usually arrive before females on breeding range.

The relevance of these findings to the 3 hypotheses on the origin of differential migration is now considered. According to the ***body size hypothesis***, larger-bodied animals winter farther north than do smaller-bodied animals. In grouse, latitudinal migrations are comparatively short (or non-existent in some species) and it is difficult to imagine a great physiological advantage accruing to those smaller migrants that winter only slightly farther south from the breeding grounds than do larger individuals. Altitudinal differences in migration were observed for white-tailed ptarmigan by Hoffman and Braun (1975) who found males wintering in sparse willow (*Salix*) cover close to the alpine breeding grounds whereas females wintered in streamside willow thickets at slightly lower elevations. This might be interpreted as support for the *body size hypothesis* but average weights of male and female white-tailed ptarmigan are virtually identical (Johnsgard 1983) and it seems unlikely that sex biases in migration distance could be driven by such slight differences in body size. In general, sex or age biases in migration distances of grouse seem far too small to be accounted for by body size differences.

The *dominance hypothesis* implies that larger or older animals, especially males, force subordinate animals to winter in habitats far from the breeding grounds. In blue grouse, migration occurs at a time of year when overt aggression is minimal. The supposedly "dominant" animals, adult males, leave breeding range before juveniles and older females. Therefore, the longer migrations of juveniles could not be a direct product of overt aggression by adult males at the time of migration. Further, I did not see aggressive interactions among juveniles or brood females in fall. There is little evidence of strong dominance interactions in autumn for other migratory grouse and the species that exhibit aggression in fall (e.g. ruffed grouse, *Bonasa umbellus*) are among the least migratory, a direct contradiction of the dominance hypothesis. Thus, I believe that differential migration in blue grouse or other tetraonines cannot easily be explained by dominance interactions.

The *arrival time hypothesis* predicts that the sex or age class with the greatest investment in territorial space will winter closest to breeding range. Blue grouse do not become closely associated with a territory until spring of their first year of life at the earliest. Movements in the first year are, at least in part, dispersive in nature as they involve searches for suitable breeding habitats which are not occupied by adults. In spring, young grouse of both sexes wander in search for available space in which to settle (Sopuck 1979, Hannon et al. 1982, Jamieson and Zwickel 1983*a*). At this time, previously established adults appear able to prevent young grouse from establishing territories nearby and where a young grouse will eventually settle is somewhat unpredictable as it depends in part on what territories have become vacant due to deaths of adults in the previous year. As it is unlikely that young birds can displace territorial adults, their best strategy is to wait until adults have settled on breeding range before returning and searching for a place to settle. Once established on a territory it likely benefits a grouse to remain as close to breeding range as possible and arrive on its territory early in spring.

Many species of grouse are thought to be polygynous or promiscuous with one male frequently mating with 2 or more females (Wiley 1974, Wittenberger 1978). Competition among males for the "best" territories, where they will be able to mate with the most females, is thought to be strong and may have led to deferred breeding in many species. Although non-breeding females are also known for some tetraonines, failure to breed is less frequent for females than males, and competition between males for suitable breeding sites is likely more intense. Therefore, males should be expected to winter closest to breeding range, as seems to be the case in most species.

Although the distances involved are much shorter, the patterns of differential migration found in grouse are similar to those reported in many other birds and seem, at present, to be best explained by the arrival time hypothesis.

The migrations of adults are goal-oriented and involve a particular geographical site as an objective. In contrast, movements of young animals, which have not previously established themselves on breeding range, may be dispersive (or "non-calculated") in nature. Therefore, a full explanation of differential migration should address the question "Why do young birds tend to disperse while older birds tend to show site fidelity?"

2.5 Summary

Migration of blue grouse was studied through radio-tracking and observing color-banded birds on Hardwicke Island, British Columbia from 1979 to 1982. Fall migration distances of juveniles varied from 0 to 12 km for males (median = 1.9 km, *N* = 34) and 0 to 15 km for females (median = 2.3 km, *N* = 76) and did not differ significantly between sexes or among years. Fall migration was not highly synchronized among all juveniles in the population; instead it was a gradual process spread over a period of 2 months or more. Timing of fall migration for juveniles may have differed among years. Age of juveniles at the time of departure from breeding range in fall averaged 114 ± SE 2 days (*N* = 85) and varied greatly among individuals (range = 65 - 155 days). In fall, juveniles showed a tendency to move eastward from the 465-ha main study area. This was especially pronounced in grouse that moved >5 km and was likely influenced by the size and shape of the island. Distances moved by juveniles in fall and spring were similar but a pattern of directionality in spring migration was detected only for grouse moving >5 km. Movements of adults and yearling grouse of both sexes were shorter than movements of juveniles (medians = 0.3 - 0.7, range = 0.0 - 5.4 km) and showed no directional pattern. The shorter movements by adults may have occurred because: (1) some juveniles settled in spring near where they had wintered, (2) some juveniles moved in their first fall but became non-migratory after first settling on breeding range, or (3) grouse that moved long distances suffered high mortality. Sex and age differences in distance of migration have been reported for several species of grouse. The present data for blue grouse and other tetraonines suggest that sex or age classes with the greatest investment in territorial space should winter closest to breeding range.

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TABLE 2.1. Differences in fall migration distances (km) of radio-marked and non-radioed blue grouse by sex and age.

		Median migration distance (*N*)		
Age	Sex	Radio	Non-radio	*P*[a]
Adult	Male	0.5 (10)	0.9 (14)	>0.10
Yearling	Male	0.2 (10)	0.5 (7)	>0.10
Ad + yrlg[b]	Female	0.4 (5)	0.4 (32)	>0.10
Juvenile	Male	1.9 (34)	1.3 (16)	<0.05
Juvenile	Female	2.3 (76)	1.5 (16)	<0.05

[a] Mann-Whitney U-test.

[b] Pooled because of small samples of radio-marked grouse.

TABLE 2.2. Annual variation in fall migration distances (km) of radio-marked juvenile blue grouse.

	Median distance (*N*)	
Year	Males	Females
1979	2.1 (9)	3.0 (14)
1980	1.9 (16)	3.6 (22)
1981	1.7 (9)	2.0 (40)
All years	1.9 (34)	2.3 (76)

TABLE 2.3. Fall migration distances (km) of adult, yearling, and juvenile blue grouse, 1979-1981.

Age	Sex	*N*	Median fall migration distance (km)	Range
Adult	Male	24	0.7	0.0 - 5.4
Adult	Female	21	0.5	0.0 - 3.7
Yearling	Male	17	0.3	0.1 - 5.4
Yearling	Female	16	0.3	0.0 - 1.6
Juvenile	Male	34	1.9	0.0 - 12.0
Juvenile	Female	76	2.3	0.0 - 15.0

TABLE 2.4. Mean date of fall migration (± SE) for radio-marked juvenile blue grouse, 1979-1981.

	Mean date of migration ± SE (*N*)	
Year	Males	Females
1979	11 Oct ± 10d (6)	23 Sep ± 7d (12)
1980	28 Sep ± 7d (15)	24 Sep ± 4d (19)
1981	18 Oct ± 9d (8)	12 Oct ± 4d (25)
All years	6 Oct ± 5d (29)	4 Oct ± 2d (56)

TABLE 2.5. Directions (°) of fall migration of adult, yearling and juvenile blue grouse, 1979-1981.

Age and sex	*N*	Mean direction (°) ± angular deviation	*r*[a]	*P*[b]
Adult and yearling males	41	199 ± 78	0.07	>0.10
Adult and yearling females	37	244 ± 70	0.25	0.10
All adults	78	234 ± 75	0.15	>0.10
Juvenile males	34	108 ± 68	0.29	0.06
Juvenile females	76	80 ± 70	0.25	<0.01
All juveniles	110	89 ± 70	0.26	<0.01
Juveniles (<5 km)	81	153 ± 80	0.03	>0.10
Juveniles (>5 km)	29	85 ± 20	0.94	<0.01

[a] Length of the mean vector, a measure of directionality.

[b] Rayleigh's test.

TABLE 2.6. Minimum over-winter survival of radio-marked juvenile blue grouse migrating "short" or "long" distances.

	Percent survival (*N*)		
Sex	Short-migrants[a]	Long-migrants[b]	*P*[c]
Male	76 (17)	35 (17)	<0.01
Female	61 (36)	40 (40)	0.07

[a] Grouse migrating <1.9 km for males, <2.3 km for females.

[b] Grouse migrating >1.9 km for males, >2.3 km for females.

[c] X^2 contingency table.

TABLE 2.7. Sex and age differences in migration distances of North American grouse.

Species	Relative distance of migration	References
White-tailed ptarmigan	adult males < juvenile males < adult females < juvenile females	Hoffman and Braun (1975)
Willow ptarmigan	males < females	Weeden (1964)
Willow ptarmigan	adult males < juvenile males < adult females < juvenile females	Irving et al. (1967)
Rock ptarmigan[a]	males < females	Weeden (1964)
Spruce grouse	males < females	Herzog and Keppie (1980)
Sage grouse	males < females	Beck (1977)
Blue grouse	females < males	Cade (1985)
Blue grouse	adults and yearlings (both sexes) < juveniles (both sexes)	this study

[a] *Lagopus mutus*; all other scientific names are given in text.

FIGURE 2.1. Distances (km) and directions (°) of fall migration for radio-marked juvenile blue grouse on Hardwicke Island, British Columbia, 1979-1981. All locations on breeding range are standardized to a common center.

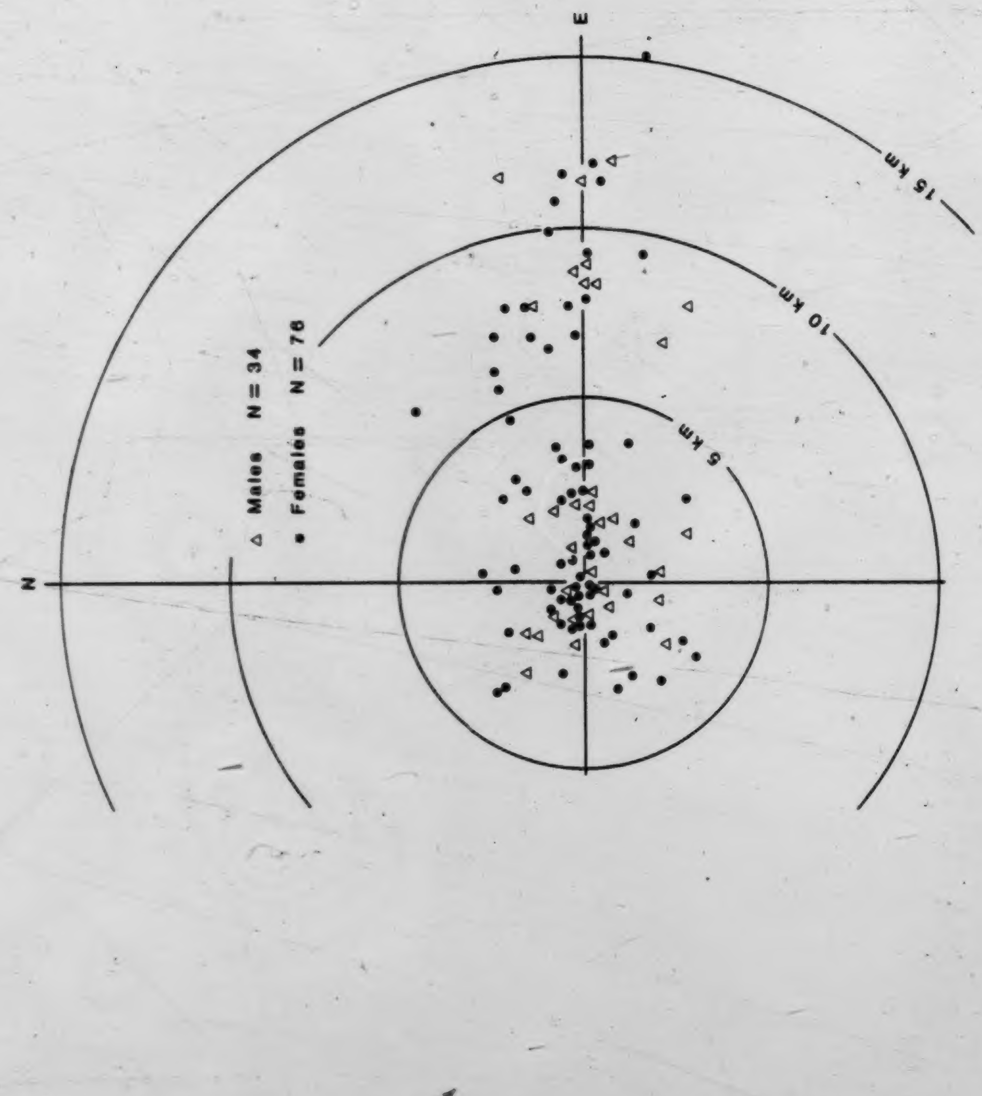

E
N
5 km
10 km
15 km
△ Males N = 34
● Females N = 76

FIGURE 2.2. Distances (km) and directions (°) of fall migration for 78 adult and yearling blue grouse on Hardwicke Island, British Columbia, 1979-1981. All locations on breeding range are standardized to a common center.

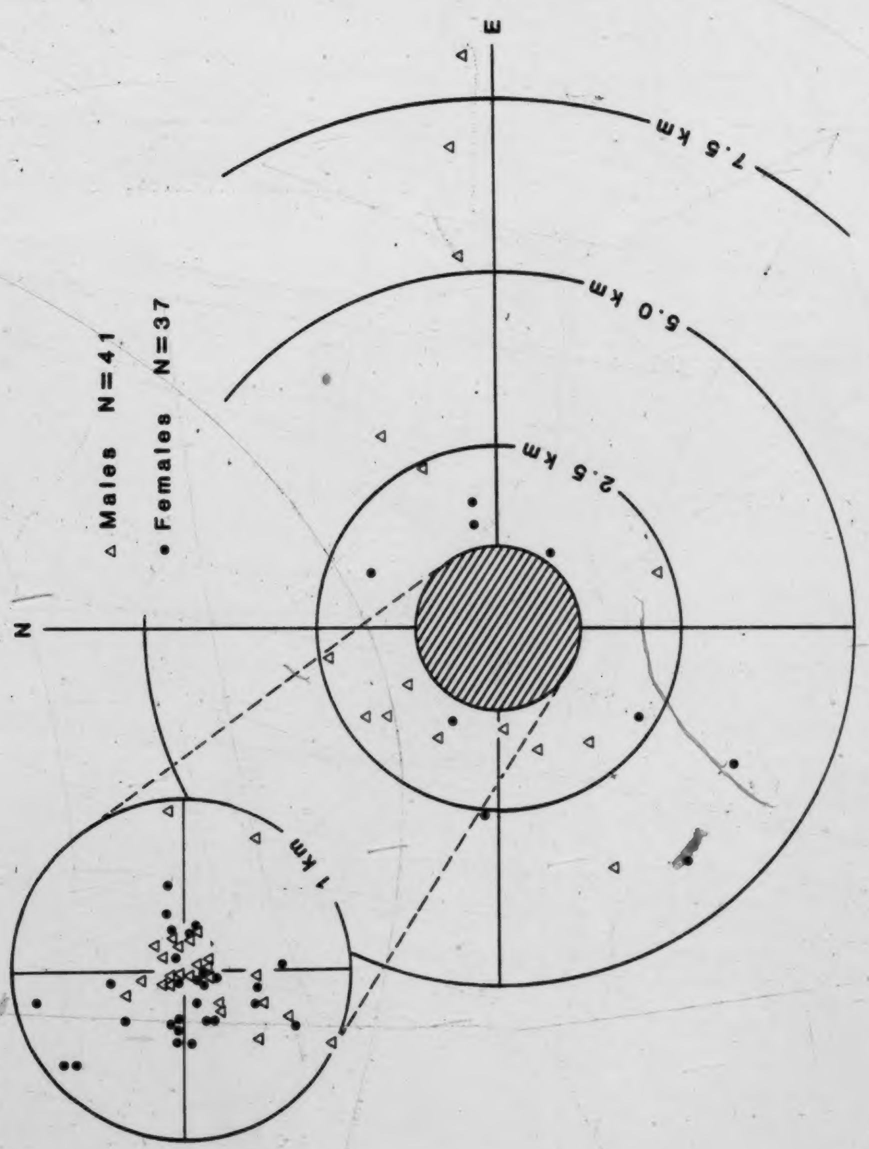

△ Males N=41
● Females N=37
N
E
1 km
2.5 km
5.0 km
7.5 km

FIGURE 2.3. Relationship of spring migration distance (km) to fall migration distance (km) for 50 radio-marked juvenile blue grouse.

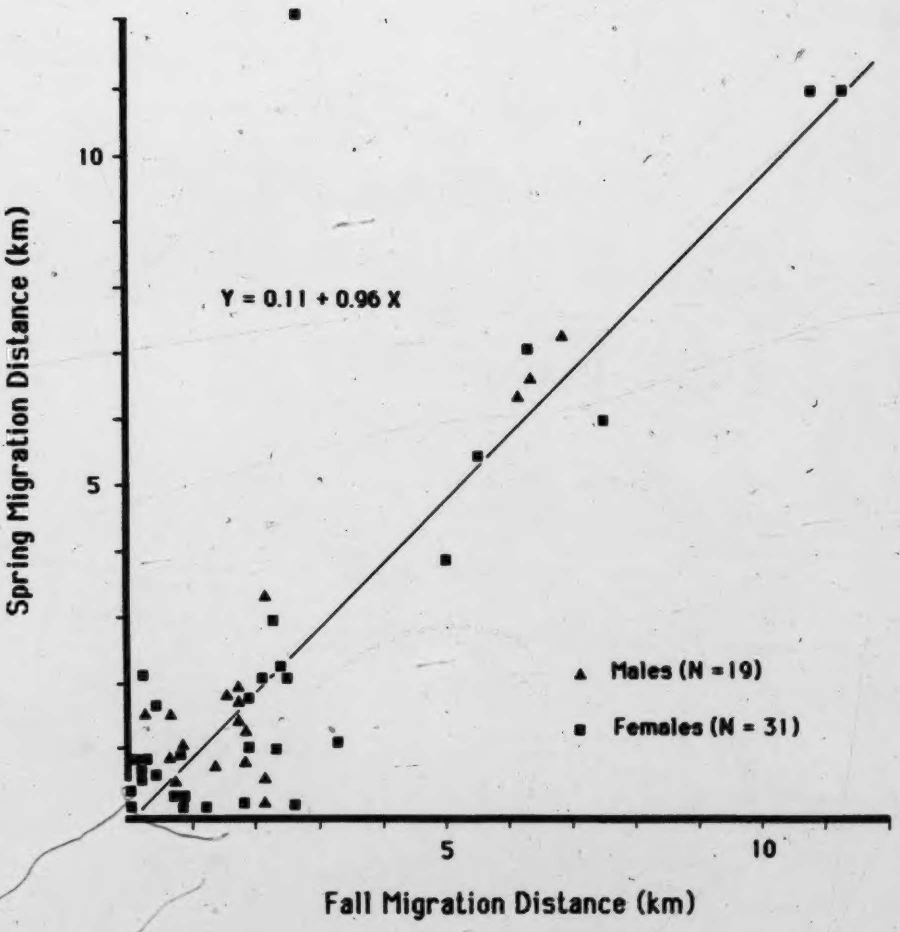

Spring Migration Distance (km)
Fall Migration Distance (km)
Y = 0.11 + 0.96 X
▲ Males (N = 19)
■ Females (N = 31)
10
5
5
10

FIGURE 2.4. The dates of fall migration for 85 juvenile blue grouse.

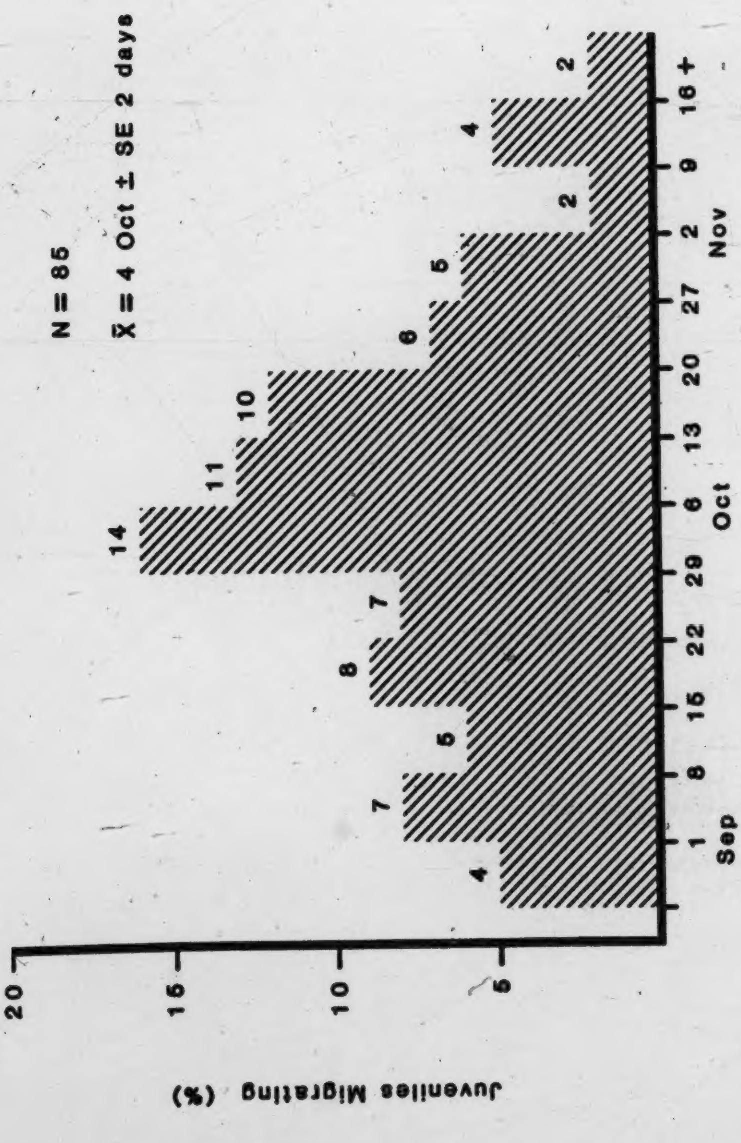
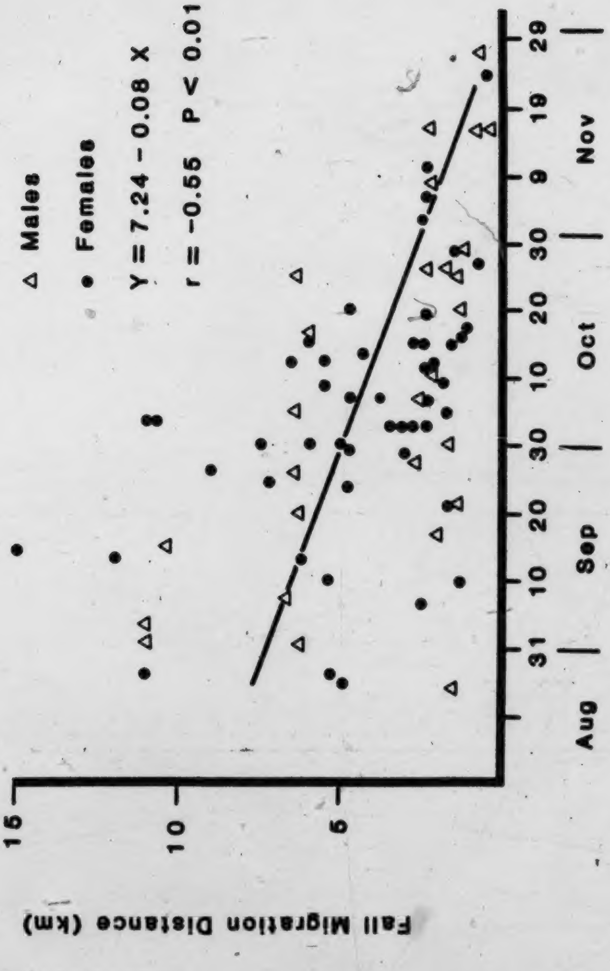

N = 85
X̄ = 4 Oct ± SE 2 days
Juveniles Migrating (%)
20
15
10
5
4
7
5
8
7
14
11
10
6
5
2
4
2
1
8
15
22
29
6
13
20
27
2
9
16+
Sep
Oct
Nov

FIGURE 2.5. The inverse relationship between fall migration distance (km) and date of migration for 76 radio-marked juvenile blue grouse for which both distance and date were determined.


△ Males
● Females
Y = 7.24 − 0.08 X
r = −0.55 P < 0.01
Fall Migration Distance (km)
15
10
5
Aug
31
10
Sep
20
30
10
Oct
20
30
9
Nov
19
29

3. WINTER HABITAT OF BLUE GROUSE ON HARDWICKE ISLAND, BRITISH COLUMBIA

3.1 Introduction

Throughout much of their range in western North America, blue grouse (*Dendragapus obscurus*) breed in open habitats and migrate in summer or fall to montane or subalpine coniferous forests where they spend the winter (Aldrich 1963, Johnsgard 1983, Bendell and Zwickel 1985). Wintering areas are largely isolated from human contact and, as a consequence, little is known about the winter habitat of blue grouse.

Fall and winter are thought to be critical periods of mortality for populations of birds in general (Lack 1954, 1966; Fretwell 1972) and grouse in particular (Bendell 1972, Watson and Moss 1979) and the kind of habitat that a grouse uses during the non-breeding season could influence its survival (Jenkins et al. 1963, Gullion and Marshall 1968, Rusch and Keith 1971). Thus, the availability of suitable winter habitat might affect the distribution and abundance of blue grouse and an understanding of winter habitat relationships may have important implications for the management and conservation of this species.

From 1979 to 1982, I studied wintering blue grouse on Hardwicke Island, British Columbia, Canada. Here, I describe the winter habitat and food of blue grouse and discuss factors that might influence habitat use. Based on a sample of radio-marked juveniles, the influence of habitat on autumn and winter survival is assessed.

3.2 Study Area and Methods

Research was conducted on Hardwicke Island (50° 25' N, 125° 50' W) located 3 km north of the village of Sayward, British Columbia, Canada. The topography of the 77-km² island is rugged with elevation ranging from sea level to over 800 m. Dominant trees are mainly conifers and vegetation is typical of the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). Much of the island has been logged or burned and consists of seral stages of 0 to 250+ years in age (Figure 3.1). Logging began in the late 1800's and was first directed at timber growing on more productive lowland sites but in recent years, much of the interior part of the island has been logged. Most remaining mature forest is on poorer soils at higher elevations. Early successional stages (<20 years in age) support an abundance of forbs (broad-leaved herbaceous plants), shrubs, ferns, and grasses, interspersed with thickets of young hemlock and plantations of Douglas-fir (*Pseudotsuga menziesii*). These seres are preferred breeding habitats and support densities of blue grouse several times greater than those in second-growth and mature forests (Niederleitner 1982).

Climate of the area is moist and temperate. During the 3 years of study, mean daily temperature from October to March at Sayward was 4° C and total precipitation averaged 120 cm (>90% occurring as rainfall). Snowfall varied greatly among years (range 23-168 cm) and averaged about 100 cm annually with slightly over half occurring in January. At sea level, snow cover usually persisted for only a few days but accumulations were far greater and more persistent at higher elevations. At elevations of 300 m or more, snow covered the ground for about 5 weeks in 1979-1980 and for more than 9 weeks in 1981-1982. In contrast, there was little snow in 1980-1981 (Anonymous 1979-1982).

General methods used to study blue grouse in coastal British Columbia have been detailed by Zwickel and Bendell (1967*a*) and Zwickel (1982). As part of a long-term population study, blue grouse were located with trained pointing dogs, captured with noosing poles (Zwickel and Bendell 1967*b*), and individually marked with colored leg-bands. In late summer and early autumn 1979-1981, 235 juveniles were equipped with radio transmitters mounted as back-pack units (Brander 1968). Radio-marked grouse were located with a portable receiver and hand-held yagi antenna; non-radioed individuals were located with a pointing dog. Most (>95%) of the radio-marked grouse were captured on a 465-ha main study area where breeding populations were being studied intensively.

Habitat type, general class of vegetation density, and elevations were recorded at each site where a grouse was observed. Habitat types were described on the basis of the dominant plants (the species providing the greatest amount of canopy cover) in both tree and ground layers of vegetation. Density of early successional vegetation was classified as: very open, open, dense or very dense after Bendell and Elliott (1966). Two older successional stages were recognized: second-growth forest (21-100 years in age) and mature forest (≥250 years in age). Only small stands of 101-250 year-old forest were present on the island and this age class was not considered to be a major habitat type. Elevation was classified as ≤150 m, 151-300 m, 301-450 m, or >450 m.

Representative stands of the 6 general classes of vegetation density were sampled in summer 1982. Canopy cover of herbaceous plants, shrubs, and mosses was recorded at 20x50-cm quadrats spaced at 10-m intervals on 100-m transects (Daubenmire 1959). Seven classes of canopy cover were recognized: <1%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, and >95%. On 60% of the transects, tree densities were recorded at 20-m intervals using the point-centered quarter method

(Cottam and Curtis 1956). Heights of shorter trees (<3 m) were measured with a meter stick and heights of taller trees were estimated. Diameter at breast height was recorded for each tree.

Preferences of grouse for different habitat types were determined by 2 methods. Earlier successional stages of the "very open" to "very dense" type were searched with a pointing dog to obtain a relative index of habitat use for grouse of each sex and age. This method was not used in second-growth and mature forest where grouse spent most of their time in trees and were not readily found by dogs. Radio-marked grouse could be found in all habitats, however, and habitat preferences of this sample were determined by comparing availability and use of different habitats. Centers of activity (Hayne 1949) of wintering radio-marked grouse and 150 random points were plotted on a 1:11900 forestry map produced by Crown Forest Products (Vancouver, British Columbia). Based on data from this map, the 2 samples were compared with regard to age of plant communities, elevation (to the nearest 30 m), and site factor (on a scale of 1 to 6). The latter was an index of productivity as indicated by the ability of the soil to grow trees. A site factor of "1" indicated that a tree would grow to 55 m or more in 100 years; a site factor of "6" indicated a tree would grow only 10-20 m in the same period. The distance of a potential winter habitat from breeding range was another factor that might have influenced habitat use. The effect of habitat proximity was evaluated by comparing the distances that grouse wintered from the center of the main study area (where most grouse were radio-marked) to distances of random points from this center.

Samples were compared with Kolmogorov-Smirnoff 2-sample tests, Kruskal-Wallis tests (Conover 1980), and discriminant analysis (Nie et al. 1975) to identify the variables with the greatest influence on habitat use and survival.

Assumptions of multidimensional normality and homogeneity of covariances underlie procedures such as discriminant analysis (Kleinbaum and Kupper 1978, Pimentel 1979) but testing such assumptions is difficult. As such tests are thought to be robust, they can be applied cautiously.

To evaluate the effect of habitat on survival, sites where radio-marked grouse died prior to migration, locations where grouse died after settling on winter range, and those in which birds survived over winter were compared. Solar-powered transmitters used during 1979-1980 and 1980-1981 functioned poorly during winter when grouse frequented dense coniferous cover. This meant that grouse dying during winter were unlikely to be found. Elimination of such animals from the sample could severely bias results (White 1983), thus grouse that disappeared on winter range were treated as dying.

Winter food habits of blue grouse were identified by microscopic analysis of fecal droppings (undertaken by the Composition Analysis Laboratory, Range Science Department, Colorado State University). Up to 3 droppings were collected per grouse observed in winter. Samples were pooled by sex-age class, homogenized by grinding over a 1-mm screen, placed on slides, and examined by microscope. Five slides were inspected for each group with only "valid fields" containing 2 or more identifiable items being used in the analyses. For each slide, the plant species present at 20 randomly-chosen valid fields were recorded. The frequency of each plant species per 100 valid fields was converted to relative density (an index of dry weight) as described by Sparks and Malechek (1968).

3.3 Results

3.3.1 Characteristics and Distribution of Different Habitat Types

When the study began, the relative abundance of different age seral stages on Hardwicke Island was: 0-10 years, 12%; 11-20 years, 9%; 21-50 years, 40%; 51-100 years, 16%; 101-250 years, 2%; and >250 years, 16% (Figure 3.1). The remaining 5% of the island was privately owned and was not classified to forest type. Logging operations reduced the amount of mature forest (and increased the area of early successional vegetation) by about 2% between 1979 and 1982.

Changes in plant succession that followed fire or clear-cut logging are summarized in Tables 3.1 and 3.2. General trends were a rapid increase in density of coniferous trees during the early stages of succession followed by a decrease in tree densities in mid succession. Tree densities again increased in mature forest as seedlings became established beneath the canopy. The basal area of trees (the total area of tree stems per ha) was greatest in second-growth forests but declined somewhat in mature forest.

Herbaceous and shrub cover was most abundant in early seral stages but decreased as coniferous cover increased and then showed a slight increase in mature forest (which has a more open canopy than second-growth forest). Mosses were most abundant in mature forest but were present also in earlier seral stages, possibly as an artifact of previously-logged forests.

Western hemlock comprised 66% of the tree cover on transects and, if recently-logged (very open) areas where Douglas-fir had been replanted are omitted, about 76% of the total trees. Douglas-fir and western red cedar (*Thuja plicata*) were common trees also, but western white pine (*Pinus monticola*), Sitka spruce

(*Picea sitchensis*), lodgepole pine (*Pinus contorta*), amabilis fir (*Abies amabilis*), red alder (*Alnus rubra*), and willow (*Salix* sp.) were less numerous (Table 3.1). Abundant understory plants included mosses, fireweed (*Epilobium angustifolium*), salal (*Gaultheria shallon*), deer fern (*Struthiopteris spicant*), sword fern (*Polystichum munitum*), and red huckleberry (*Vaccinium parvifolium*) (Table 3.2).

3.3.2 General Description of Habitat Use

Between 1 November and the time of spring migration (approximately 1 March for males and 1 April for females), dominant tree and ground cover was recorded for sightings of 1100 grouse. Western hemlock was the dominant tree at 94%, Douglas-fir at 5%, and other species (red alder, amabilis fir, and western red cedar) at 1% of these locations. Snow was the predominant form of ground cover at 32% of the winter sightings. Mosses (17%), salal (10%), sword fern (10%), dead grasses (9%), red huckleberry (7%), woody debris (4%), deer fern (3%), dead fireweed (3%), salmonberry (*Rubus spectabilis*) (3%), and a variety of other species (<3%) followed in occurrence.

Comparable data on habitat use by all sex-age classes were not available for radio-marked grouse as few older birds were radio-marked and they were located less frequently than juveniles. Consequently, comparisons among adult males, adult females, juvenile males, and juvenile females were based primarily on the sample of grouse located by dog. These data mainly represent grouse living in earlier successional stages as grouse living in successional stages older than 20 years were not readily located by means other than radio-tracking. General differences in habitat use by the 4 sex-age classes are summarized in Figures 3.2 and 3.3. Statistical comparisons in the form of X^2 contingency tables revealed significant ($P < 0.01$) in vegetation density and elevation of habitats used by the different sex-age classes (grouse of unknown age were not included in these analyses). Pairwise contrasts indicated that females tended to live at lower elevations and in denser coniferous cover than males but there were no significant differences ($P > 0.05$) between adults and juveniles within a given sex. Similar comparisons involving pooled samples of all males and females (adults, juveniles, and age undetermined) indicated that the sexes used different elevations and densities of vegetation ($P < 0.01$ in both instances).

3.3.3 Habitat Preferences of Radio-marked Grouse

Mortality of juvenile blue grouse was high during summer and autumn and only 110 of 235 radio-marked juveniles were known to settle on winter range. Seven of these grouse left Hardwicke Island and settled on nearby parts of the mainland and 2 others could not be associated with any particular habitat type. In total, 101 juveniles were assigned to specific winter habitats.

Juveniles wintered in habitats ranging from 4 to 250+ years in age. Kolmogorov-Smirnoff 2-sample tests suggested that ages of habitats used by grouse differed from those expected by chance (Table 3.3). A more detailed inspection of the data (Figure 3.4) indicated that grouse preferred mature forests for wintering, used earlier successional stages (<20 years in age) extensively, and avoided mid-successional stages (51-250 years in age). Avoidance of mid-successional stages may occur sooner than indicated in Figure 3.4 because 15 of 27 grouse found in the 21-50 year class of vegetation lived in habitats less than 30 years in age.

Although juveniles wintered at a broad range of elevations (Figure 3.4), they tended to select higher locations (>300 m). Site factors, which indicate the relative productivity of the soil, also may have differed between wintering sites and random points, with grouse selecting areas of relatively low productivity (Table 3.3, Figure 3.4). This result also might be attributed to the preference of blue grouse for mature forests and the fact that much of the remaining mature forest on Hardwicke Island was on poorer quality sites. On average, wintering sites were nearer the study area than expected by chance (Table 3.3). Thus, the distance of a potential wintering area from breeding range influenced its probability of being used by grouse (Figure 3.4).

The 4 habitat variables considered here are highly intercorrelated because of the pattern in which the island was logged. For example, lowland sites tended to be more productive and usually supported second-growth forest whereas higher elevations tended to have poorer soils and mature forest. Thus, grouse might have settled most frequently at higher elevations because: (1) they preferred higher elevations, (2) they preferred mature forest, or (3) they avoided areas with richer soils. Multivariate analyses provide a way of separating the effects of such intercorrelated variables; hence, the variables habitat age, elevation, site factor and distance from breeding range were included in a discriminant analysis. All variables except site factor ($P > 0.10$) were important in separating random points from wintering sites ($P < 0.01$).

Comparisons of habitat preferences of radio-marked juvenile males and females indicated that the 2 sexes preferred habitats at different elevations but were similar with regard to age of the community, site factor, and distance from breeding range (Table 3.4).

The general characteristics of habitats used by 19 radio-marked adults were recorded. All adult males ($N = 14$) were found at elevations of 300 m or more. Seven inhabited successional stages ≤ 20 years in age, 3 lived in second-growth forest (>20 years in age), and 4 lived in mature forest. Three adult females were found below 300 m in elevation and 2 others were found above 300 m. Three females frequented early seral stages and 2 lived in second-growth forest. Overall, radio-marked adults showed the same general pattern of habitat selection as juveniles with males wintering at higher elevations and both sexes using a broad range of successional stages.

3.3.4 Habitat Characteristics and Survival Over Winter

Much of the mortality of radio-marked grouse occurred early in autumn before juveniles had left breeding range. This mortality might have been a product of the habitat that grouse were living in at this time. Habitats in which grouse survived over winter, those in which grouse died after migration, and those in which grouse died prior to migration were compared with a Kruskal-Wallis test (Table 3.5). The 3 samples differed with regard to habitat age, site factor, elevation, and distance from the main study area. Seven of the 8 significant pairwise contrasts ($P < 0.05$) involved differences between habitats in which grouse died prior to migration indicating there were substantial differences between sites of pre-migration deaths and winter habitat but little difference in habitats used by survivors and non-survivors in winter (Table 3.5).

3.3.5 Winter Food Habits

Analysis of fecal droppings collected from 120 grouse indicated that western hemlock and Douglas-fir were the 2 major winter foods (Table 3.6). Food habits seemed to vary among sex-age classes with adult males eating mainly hemlock and juveniles preferring Douglas-fir needles (this could not be evaluated statistically as samples for each sex and age were pooled before analysis).

3.4 Discussion

The use of winter habitat by blue grouse on Hardwicke Island differed somewhat from that reported for other regions. In the western United States, blue grouse are often associated with Douglas-fir or true fir (*Abies* spp.) forests that occur at higher elevations (Marshall 1946, Wing 1947, Caswell 1954, Standing 1960, Aldrich 1963, Zwickel et al. 1968). Based on a general survey covering much of the geographical range of the species, Bendell and Zwickel (1985) concluded that blue grouse used a number of different coniferous species for winter food and shelter and that habitat tolerances were much broader than indicated in previous studies. Similarly, a recent study by Cade (1985) indicated that blue grouse winter in a broad range of coniferous habitats in Colorado.

On Vancouver Island, King (1971) found adult male blue grouse wintering in subalpine forest, especially in open stands of mountain hemlock (*Tsuga mertensia*), but was unable to find adult females or juveniles on winter range. Limited evidence from the same region indicated that females and juveniles may use forests at lower elevations for wintering (Sopuck 1979). My results support this view as both adult and juvenile females occurred at lower elevations on average than adult and juvenile males. The reason for this segregation is not clear but it occurs also in white-tailed ptarmigan (*Lagopus leucurus*) (Hoffman and Braun 1975). Data obtained from grouse located by dog (but not those located by radio) suggested that female blue grouse tended to use different successional stages than males. This result might be spurious, reflecting a propensity for males to use sites at higher elevation (many of which had been logged in recent years). Sex differences in habitat use have been reported for other species of grouse including capercaillie (*Tetrao urogallus*) (Koskimies 1957) and white-tailed ptarmigan (Hoffman and Braun 1975), although in the latter instance it was attributed to the fact that the sexes migrate different distances and thus are apt to settle in different kinds of habitat.

Wintering blue grouse on Hardwicke Island were tolerant of a broad range of habitat conditions in terms of vegetation structure and successional stage. Heights of coniferous cover used in winter ranged from <1 to >50 m and ages of habitats varied from 4 to >250+ years. A characteristic common to all habitats used by blue grouse was the presence of western hemlock which provided much of the winter food and cover.

Studies of ruffed grouse (*Bonasa umbellus*) in Minnesota (Gullion and Marshall 1968) and Alberta (Rusch and Keith 1971) as well as red grouse (*Lagopus lagopus scoticus*) in Scotland (Jenkins et al. 1963) suggest that fall-winter habitat selection may influence over-winter survival. My data are equivocal on this matter for although many grouse died in open, early-successional stages before migration had occurred, there was little difference between habitats used by survivors and non-survivors after migration. Two other events also occur at the time of year when many juveniles die: (1) migrating raptors peak in numbers and (2) broods of blue grouse break up. Perhaps, as much as being an influence of habitat, the high mortality of grouse on breeding range reflected predator response to high densities of young birds or the naivety of young grouse which had separated from their mothers and brood-mates.

3.5 Summary

Habitat use by wintering blue grouse was studied on Hardwicke Island, British Columbia, Canada. Western hemlock was the dominant tree at 94% of all sites where grouse were observed in winter; snow and a variety of shrubs, herbaceous plants, and mosses were dominant forms of ground cover. Hemlock and

Douglas-fir needles comprised most of the winter food. Habitat preferences were studied for 101 radio-marked juveniles. These grouse used a broad range of successional stages ranging from 4 to >250 years in age that supported trees from 1 to >50 m in height. Mature forest (>250 years old) was preferred winter habitat, early successional stages (≤20 years in age) were used frequently, and mid-successional stages (21-100 years in age) were less frequently used. Juveniles wintered at higher elevations and closer to breeding range than expected by chance with males wintering at higher elevations than females. Habitat preferences of a small sample of radio-marked adults were similar to juveniles. A sample of non-radioed grouse of all ages indicated that males and females differed in elevation and possibly, density (=age) of habitats used but there were no differences between adults and juveniles of a given sex. Mortality of grouse living in early successional stages was high in fall but after fall migration was completed, survival did not seem to be influenced by habitat.

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TABLE 3.1. Tree cover found in different successional stages on Hardwicke Island, British Columbia.

Parameter	Very open (*N* = 10)[a]	Open (*N* = 6)	Dense (*N* = 6)	Very dense (*N* = 4)	Second growth (*N* = 6)	Mature (*N* = 4)
Mean age of habitat (years)	7.3 (4 - 12)[b]	8.8 (5 - 15)	14.2 (5 - 20)	15.2 (13 - 19)	54.3 (44 - 58)	>250
Density (trees per ha)[c]	1462	3086	5514	11719	1712	3673
Basal area (m^2 per ha)	0.5	1.2	13.8	36.2	63.0	38.0
Height of trees (m)	1.3	1.4	2.1	2.5	-	-
Percent frequency						
Tsuga heterophylla	40.0	60.8	66.7	82.5	83.3	87.5
Pseudotsuga menziesii	50.5	7.5	3.3	2.5	3.3	1.2
Thuja plicata	5.5	27.5	24.2	15.0	5.0	10.0
Salix sp.	1.0	1.7	5.0	-	-	-
Picea sitchensis	0.5	-	-	-	5.0	-
Pinus contorta	1.0	-	-	-	1.7	1.3
Alnus rubra	1.0	-	-	-	0.8	-
Abies amabilis	-	2.5	-	-	-	-
Pinus monticola	0.5	-	0.8	-	-	-
Unidentified	-	-	-	-	0.8	-

[a] Number of transects.

[b] Range in parentheses.

[c] Estimated by the point-centered quarter method of Cottam and Curtis (1956).

TABLE 3.2. Ground cover (%) occurring in different successional stages on Hardwicke Island, British Columbia.

	Very open			Open			Dense			Very dense			Second growth			Mature		
	(*N* = 20)[a]			(*N* = 12)			(*N* = 12)			(*N* = 6)			(*N* = 6)			(*N* = 4)		
Cover (%)[b]	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq
Total plant cover	35.1	1.9	92.5	34.1	2.5	93.3	37.9	2.7	96.7	23.3	4.0	65.0	27.5	3.3	98.3	56.2	6.7	100.0
Herbaceous and shrub cover	27.5	1.7	86.5	27.7	2.4	82.5	28.8	2.5	83.3	16.8	3.2	50.0	4.8	1.6	23.0	12.3	3.2	80.0
Mosses	14.8	1.6	88.0	9.1	1.3	93.3	13.3	1.7	96.7	6.2	2.2	50.0	24.9	3.1	100.0	53.2	6.6	100.0
Woody debris	32.2	2.1	83.5	34.5	2.4	94.2	28.7	2.5	86.7	18.2	3.5	41.7	27.5	2.9	98.3	6.4	2.0	60.0
Epilobium angustifolium	8.4	0.9	49.0	4.8	0.9	35.0	0.9	0.3	12.5	0.5	0.3	8.3	-	-	-	-	-	-
Gaultheria shallon	8.4	1.3	24.0	5.7	1.6	15.0	11.1	1.9	40.8	6.4	1.8	25.0	2.1	1.1	6.7	4.6	2.7	10.0
Miscellaneous grasses	0.9	0.2	17.5	1.2	0.3	28.3	0.5	0.2	12.5	0.1	0.1	3.3	-	-	-	-	-	-
Struthiopteris spicant	2.9	0.7	15.5	6.2	1.4	26.7	5.4	1.1	25.8	0.8	0.4	6.7	1.0	1.0	1.7	-	-	-
Polystichum munitum	1.1	0.3	7.5	3.5	0.9	16.7	3.4	0.9	16.7	2.6	1.3	13.3	0.7	0.6	3.3	-	-	-
Woodsia sp.	0.9	0.3	10.0	5.6	1.1	30.8	2.1	0.7	14.2	0.3	0.3	5.0	-	-	-	-	-	-
Pteridium aquilinum	0.3	0.2	1.0	1.6	0.6	6.7	2.2	1.0	7.5	-	-	-	-	-	-	-	-	-
Carex spp.	0.3	0.1	3.0	+	+	1.7	0.2	0.1	5.0	+	+	1.7	-	-	-	-	-	-
Juncus sp.	0.4	0.2	4.0	0.3	0.2	5.0	0.1	0.0	3.3	-	-	-	-	-	-	-	-	-
Equisetum sp.	0.3	0.1	6.0	+	+	2.5	1.0	0.3	14.2	-	-	-	-	-	-	-	-	-

continued

TABLE 3.2 (Continued)

	Very open			Open			Dense			Very dense			Second growth			Mature		
Cover (%)	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq	$\bar{X}$	SE	Freq
Cirsium sp.	+	+	0.5	+	+	0.8	-	-	-	+	+	1.7	-	-	-	-	-	-
Hypochaeris radicata	2.4	0.4	27.5	0.8	0.3	15.0	0.6	0.2	10.0	-	-	-	-	-	-	-	-	-
Cornus canadensis	0.7	0.3	5.5	-	-	-	0.1	0.1	0.8	-	-	-	-	-	-	0.6	0.4	13.3
Vaccinium parvifolium	0.6	0.3	5.0	2.1	1.0	8.3	1.5	0.6	8.3	2.3	1.5	5.0	1.2	0.5	13.3	3.0	1.1	4.3
Anaphalis magaritacea	1.0	0.3	9.5	1.0	0.4	10.0	0.1	0.0	2.5	-	-	-	-	-	-	-	-	-
Rubus ursinus	0.4	0.2	4.5	0.1	0.1	0.8	0.2	0.1	2.5	-	-	-	-	-	-	-	-	-
Rubus leucodermis	0.2	0.1	2.0	+	+	0.8	-	-	-	-	-	-	-	-	-	-	-	-
Rubus spectabilis	0.2	0.1	2.5	0.9	0.6	3.3	0.1	0.1	1.7	-	-	-	-	-	-	-	-	-
Rubus parvifloris	0.4	0.3	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Linnaea borealis	0.4	0.3	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fragaria sp.	+	+	2.0	+	+	0.8	0.2	0.1	5.0	-	-	-	-	-	-	-	-	-
Vaccinium ovalifolium	0.3	0.3	0.5	+	+	0.8	0.1	0.1	0.8	+	+	1.7	-	-	-	4.4	2.0	26.7
Epilobium lactiflorum	+	+	0.5	-	-	-	+	+	0.8	-	-	-	-	-	-	-	-	-
Typha latifolia	-	-	-	-	-	-	0.2	0.1	1.7	-	-	-	-	-	-	-	-	-
Galium aparine	-	-	-	-	-	-	0.1	0.0	1.7	-	-	-	-	-	-	-	-	-

[a] Number of transects.

[b] Estimates of canopy cover based on the Daubenmire (1959) method. Only plants occurring in 1% or more of the quadrats in at least 1 successional stage are included.

+ indicates <0.1% cover.

TABLE 3.3. Characteristics of 101 wintering sites used by juvenile blue grouse and 150 randomly-located points on Hardwicke Island, British Columbia.

	Random points (N = 150)			Wintering sites (N = 101)			
Parameter	$\bar{X} \pm SE$	Median	Range	$\bar{X} \pm SE$	Median	Range	P[a]
Age (years)	66 ± 7	41	1 - 250+	92 ± 11	26	4 - 250+	0.06
Elevation (m)	234 ± 12	213	0 - 790	333 ± 12	305	60 - 670	<0.01
Site factor	3.4 ± 0.1	3.0	2.0 - 6.0	3.6 ± 0.1	4.0	2.0 - 6.0	0.08
Distance from breeding range (km)	3.9 ± 0.2	3.7	0.2 - 9.5	2.6 ± 0.2	1.9	0.3 - 7.3	<0.01

[a] Kolmogorov-Smirnoff 2-sample test.

TABLE 3.4. Characteristics of wintering sites used by radio-marked juvenile male and juvenile female blue grouse on Hardwicke Island, British Columbia.

	Juvenile males (N = 31)			Juvenile females (N = 70)			
Parameter	$\bar{X} \pm SE$	Median	Range	$\bar{X} \pm SE$	Median	Range	P[a]
Age (years)	107 ± 21	24	6 - 250+	85 ± 12	26	4 - 250+	0.90
Elevation (m)	388 ± 22	396	180 - 670	309 ± 14	305	60 - 580	0.02
Site factor	3.7 ± 0.1	4.0	3.0 - 5.0	3.6 ± 0.1	3.5	2.0 - 6.0	0.99
Distance from breeding range (km)	2.8 ± 0.4	1.9	0.6 - 7.2	2.5 ± 0.2	1.9	0.3 - 7.3	0.84

[a] Kolmogorov-Smirnoff 2-sample test.

TABLE 3.5. Characteristics of habitats where radio-marked juvenile blue grouse successfully over-wintered and habitats where juveniles died before or after migration.

	Died before migration (N = 65)		Died after migration (N = 50)		Survived over winter (N = 51)		
Parameter	$\bar{X}$ ± SE	Median (range)	$\bar{X}$ ± SE	Median (range)	$\bar{X}$ ± SE	Median (range)	P[a]
Age (years)	22 ± 6	11 (2 - 250+)	112 ± 16	43 (6 - 250+)	72 ± 14	19 (4 - 250+)	<0.01
Elevation (m)	229 ± 6	213 (150 - 370)	318 ± 19	305 (60 - 670)	348 ± 16	366 (150 - 550)	<0.01
Site factor	3.2 ± 0.1	3.0 (3.0 - 5.0)	3.7 ± 0.1	4.0 (2.0 - 6.0)	3.6 ± 0.1	4.0 (2.0 - 6.0)	<0.01
Distance from breeding range (km)	0.7 ± 0.1	0.7 (0.0 - 2.3)	2.9 ± 0.3	2.2 0.4 - 7.3	2.3 ± 0.3	1.6 (0.3 - 7.3)	<0.01

[a] Kruskal-Wallis test.

TABLE 3.6. The percentage of different plants in the winter diet of blue grouse as indicated by plant remains found in fecal droppings.[a]

Plant species	Adult male (*N* = 20)[b]	Juvenile male (*N* = 12)	Age unknown male (*N* = 8)	Adult female (*N* = 12)	Juvenile female (*N* = 24)	Age unknown female (*N* = 4)	Unknown age and sex (*N* = 40)	Mean for all grouse (*N* = 120)
Tsuga	92.9[c]	20.3	78.9	36.5	22.8	60.5	87.7	57.1
Pseudotsuga	6.0	72.4	7.1	62.2	70.4	34.7	9.5	37.5
Abies	0.6	2.8	1.1	–	–	–	–	0.7
Ferns[d]	0.6	4.4	12.6	1.4	6.8	4.8	2.5	4.7
Forbs[d]	–	–	–	–	–	–	0.3	<0.1
Equisetum	–	–	0.3	–	–	–	–	<0.1
Total	100.1	99.9	100.0	100.1	100.0	100.0	100.0	100.0

[a] See text for methodology.

[b] Number of grouse.

[c] Percent of total food.

[d] Species not identified.

FIGURE 3.1. The distribution of different successional stages on Hardwicke Island, British Columbia.

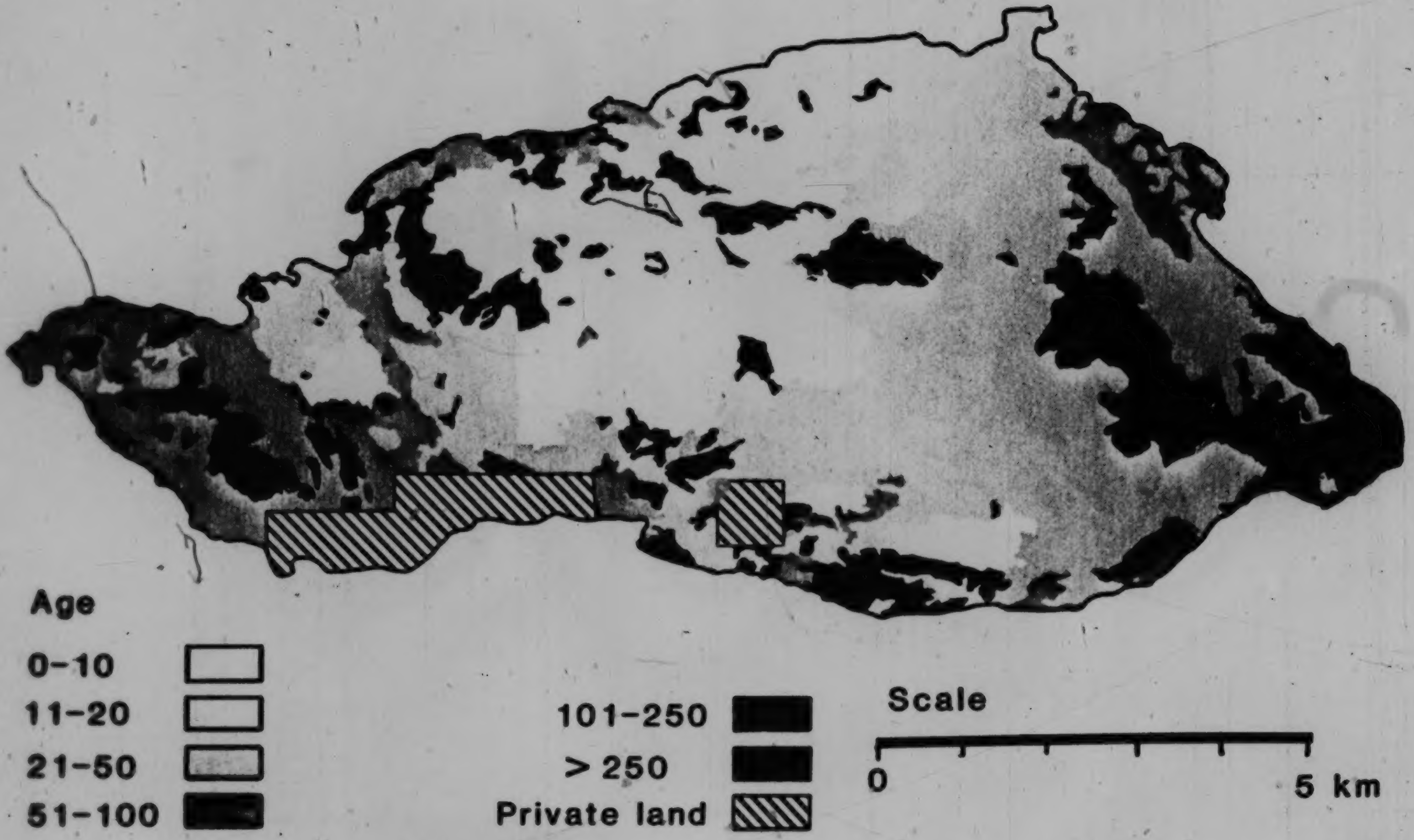

Age
0–10 ☐
11–20 ☐
21–50 ☐
51–100 ■
101–250 ■
> 250 ■
Private land ▨
Scale
0
5 km

FIGURE 3.2. Numbers of grouse sighted at elevations less than 300 m or greater than 300 m. Data are for grouse located by means other than radio-tracking. Sample sizes are indicated above the histograms. AM indicates adult males, JM - juvenile males, TM - total males (adult, juvenile, and age unknown), AF - adult females, JF - juvenile females, and TF - total females.

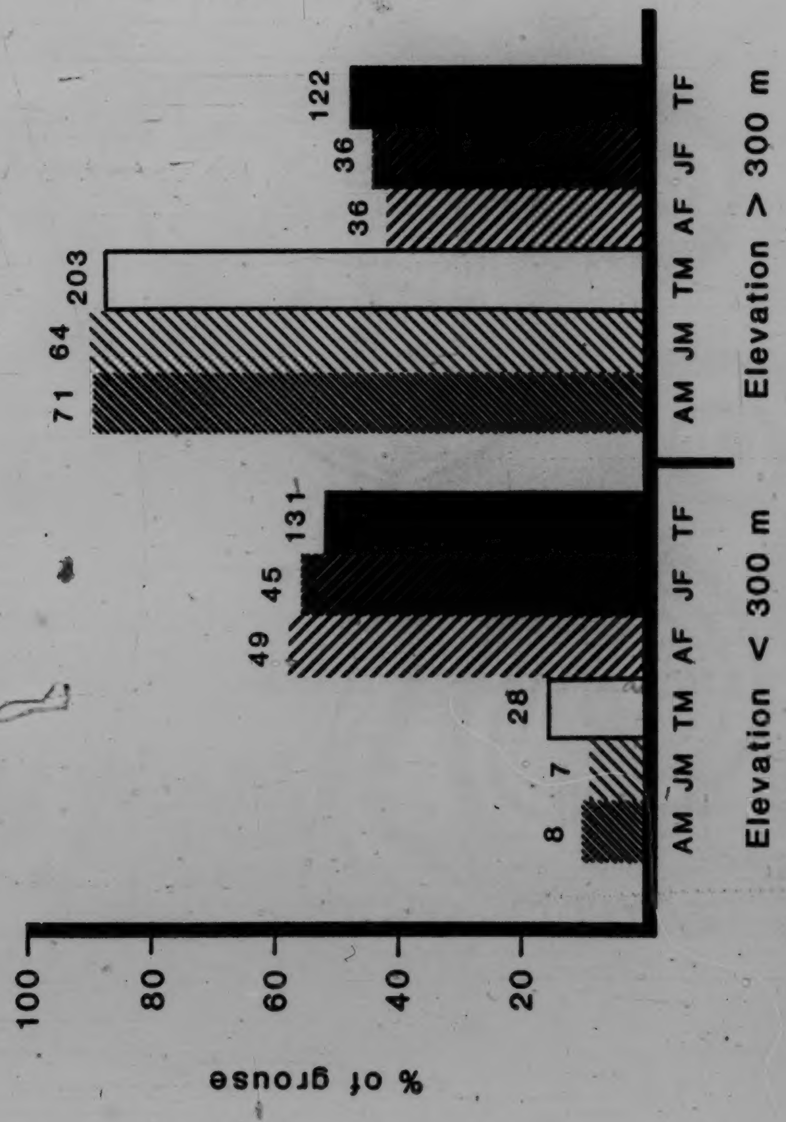

% of grouse
100
80
60
40
20
8
7
28
49
45
131
71
64
203
36
36
122
AM JM TM AF JF TF
AM JM TM AF JF TF
Elevation < 300 m
Elevation > 300 m

FIGURE 3.3. Numbers of grouse (by sex and age) observed in habitats of different vegetation density. Data are for grouse located by means other than radio-tracking. Sample sizes are indicated above the histograms. AM indicates adult males, JM - juvenile males, TM - total males (adult, juvenile, and age unknown), AF - adult females, JF - juvenile females, and TF - total females.

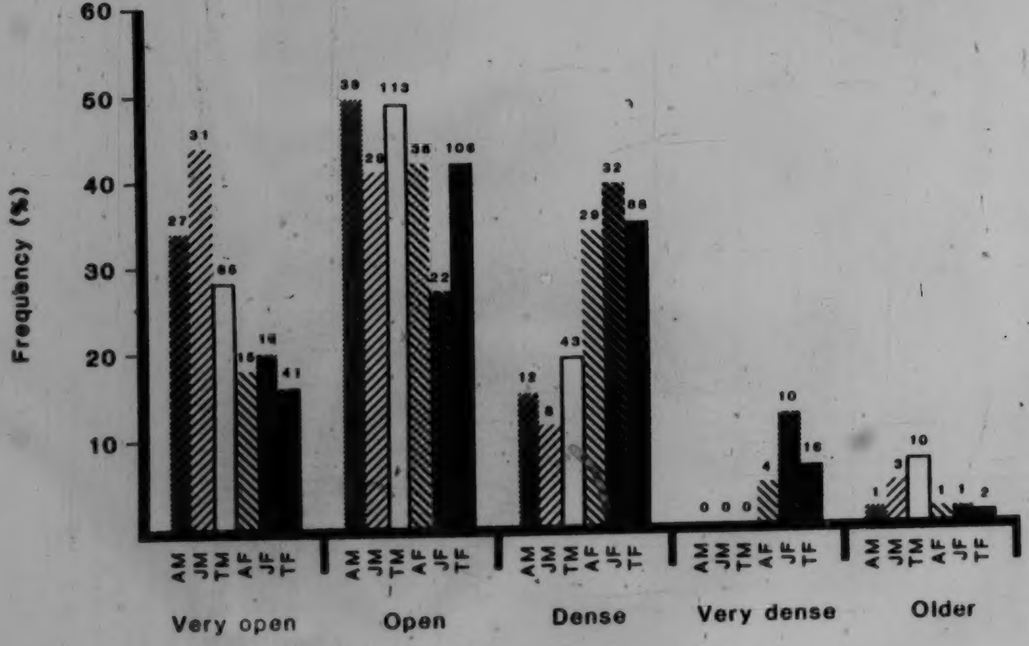
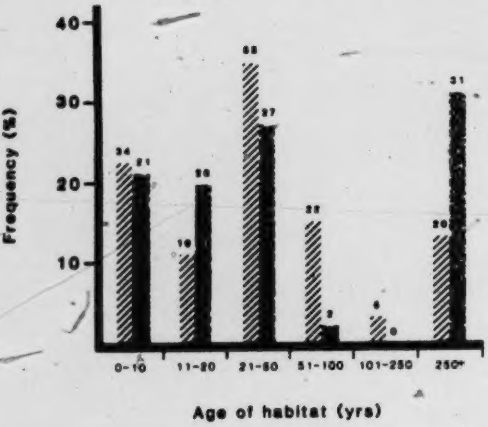
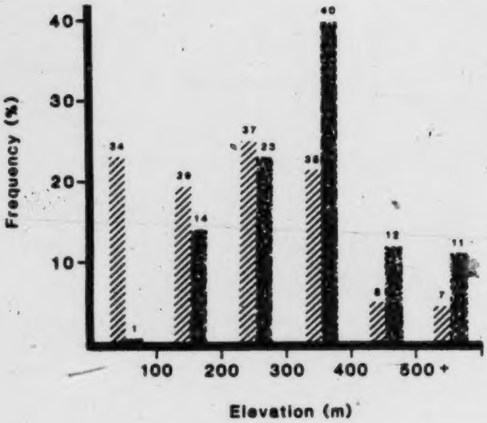
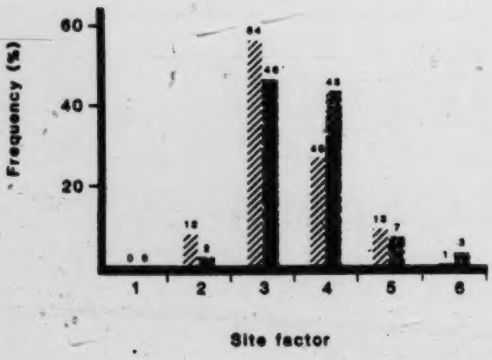
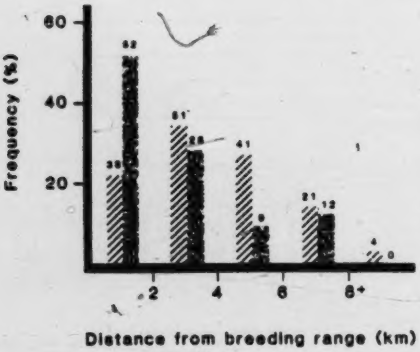

Frequency (%)
60
50
40
30
20
10
27
31
66
15
16
41
39
28
113
36
22
106
12
8
43
29
32
88
0 0 0
4
10
16
1
3
10
1
1
2
AM JM TM AF JF TF
AM JM TM AF JF TF
AM JM TM AF JF TF
AM JM TM AF JF TF
AM JM TM AF JF TF
Very open
Open
Dense
Very dense
Older

FIGURE 3.4. Characteristics of the habitat at 150 random points and 101 centers of activity of radio-marked juvenile blue grouse during winter. Cross-hatching indicates data from random points, stippling indicates data for centers of activity.


Frequency (%)
40
30
20
10
34
21
16
20
53
27
23
2
6
0
20
31
0-10
11-20
21-50
51-100
101-250
250+
Age of habitat (yrs)


Frequency (%)
40
30
20
10
34
1
29
14
37
23
32
40
8
12
7
11
100
200
300
400
500 +
Elevation (m)


Frequency (%)
60
40
20
0
0
12
2
84
46
40
43
13
7
1
3
1
2
3
4
5
6
Site factor


Frequency (%)
60
40
20
33
52
51
28
41
9
21
12
4
0
2
4
6
8+
Distance from breeding range (km)

4. SOCIAL ORGANIZATION, MOVEMENTS, AND HOME RANGES OF BLUE GROUSE IN FALL AND WINTER

4.1 Introduction

Studies of the social organization of grouse and other birds have emphasized the breeding season with mating systems drawing particular attention (Wiley 1974, Wittenberger 1978, Oring 1982). The non-breeding season is thought to be a critical period for mortality in avian populations (Lack 1954, 1966; Bendell 1972; Fretwell 1972) and selective pressures during fall and winter might be important in shaping the pattern of avian sociality.

During winter, many species of grouse tend to form flocks of one sex. A possible proximate explanation of this segregation is that the sexes migrate different distances or prefer different kinds of habitats and are not in contact with each other during winter (Koskimies 1957, Weeden 1964, Irving et al. 1967, Hoffman and Braun 1977, and others). Another possibility is that males and females avoid each other or that members of the same sex are attracted to each other (de Vos 1983). The relative importance of any of these factors in determining the fall and winter sociality of grouse has received little attention as winter studies are seldom undertaken and it is difficult to identify different sex-age classes in the field.

From 1979-1982, I studied blue grouse (*Dendragapus obscurus*) wintering on Hardwicke Island, British Columbia, Canada. In this report, I describe groupings, movements, and home ranges of grouse during fall and winter. The data for blue grouse are then compared to information on other grouse in an attempt to identify which ecological conditions lead to flocking and what factors influence the segregation of the sexes during winter.

4.2 Study Area and Methods

Hardwicke Island (50° 28' N., 125° 50' W) is situated in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). Much of the 77-km² island has been logged or burned in the past 100 years with a variety of successional stages resulting. Breeding densities of coastal blue grouse reach peak numbers in open areas created by logging or fire but plant succession occurs rapidly in such openings and, about 20 years after disturbance, dense coniferous cover again prevails, herbaceous cover decreases, and numbers of blue grouse decline (Zwickel and Bendell 1972, Niederleitner 1982). On Hardwicke Island, most blue grouse wintered in early seral stages or mature forest and seemed to avoid dense, second-growth forests (Hines 1986*b*).

General methods used in the studies of coastal blue grouse were described by Zwickel and Bendell (1967*a*) and Zwickel (1982). From late April until late August, a 465-ha study area consisting mainly of early successional stages (<15 years in age) was searched by census crews of 2 or 3 people. Grouse were located with pointing dogs, captured with noosing poles (Zwickel and Bendell 1967*b*), and individually marked with colored leg-bands. In late summer and fall 1979-1981, 235 juvenile grouse were equipped with radio packages similar to those described by Brander (1968). Most of the marked grouse observed during the present study were captured originally on breeding range.

Fall and winter field work, which was conducted over much of the island, lasted from 1 September until 31 March in 1979-1980 and 1981-1982, and from 1 September until 12 December in 1980. Radio-marked grouse were located with a portable receiver and yagi antenna; non-radioed grouse were found with a pointing dog. For many sightings of both radioed and non-radioed grouse, the surrounding area was searched thoroughly with a dog to determine if other grouse were present. A bird was said to be alone if no other grouse was found within a 10-m radius of it. The criterion used in this definition was arbitrary but increasing this distance somewhat would not appreciably change the results -- grouse were seldom found 11-50 m from each other. Sightings of 2 or more individuals were said to be of "flocks", "groups", or "aggregations". Although I use these 3 terms interchangeably, it is not known whether groupings are true flocks in the sense of being cohesive social units. Grouse that were located in tall trees or without the aid of a dog were omitted from analyses of fall and winter groupings as the presence or absence of other birds usually could not be determined under such conditions. The sex of blue grouse was readily determined in the field because males and females differ greatly in size and plumage. In winter, the body size and plumage of a juvenile is similar to that of an older bird of the same sex, so age could only be determined when a grouse was captured or identified by its colored leg-bands. For analytical purposes, grouse of 2 different age classes were recognized: (1) juveniles - hatched in the previous summer (<11 months in age), and (2) adults - all older birds. Sample sizes were not sufficient to allow subdivision of the data into adult and yearling categories.

When juveniles were individually identified during fall and winter, I attempted to determine if they were with their mothers or siblings. For this purpose, the "probable" mother of a juvenile was defined as the female with which the juvenile was first sighted in summer. Juveniles having the same probable mother were treated as siblings.

Two measurements of movement patterns of radio-marked grouse were made: daily movements and home range sizes. A *daily movement* was the straight-line distance between the location of an individual on one day and its location on the following day. *Home range size*, the total area used by an animal during winter, was determined by the minimum area method (Mohr 1947) for grouse that had settled on winter range and were located 10 or more times after 1 November.

Statistical analyses involved comparisons of frequencies with contingency tables followed by pairwise contrasts (Brown 1974) when the overall X^2 value was significant ($P < 0.05$).

4.3 Results

4.3.1 Brood Break-up

Virtually all juveniles sighted in July or early August, were in broods and were associated with older females. By late August, some broods had started to disband and by the end of September most juveniles had separated from adult females (Figure 4.1). Because of brood break-up, only a small sample of juveniles whose mothers were known were found together in fall and winter. In September, 49% of these juveniles were found with siblings, the remaining 51% were with non-sibs ($N = 49$). After 1 October, no juveniles were found with either brothers or sisters ($N = 73$). Thus, brood break-up was likely completed by 1 October.

4.3.2 Formation of Fall and Winter Flocks

The tendency for grouse to aggregate decreased throughout fall and was lowest in November for both males and females (Figure 4.2). This decline in flocking was likely a function of brood break-up. After November, flocking again increased and peaked in January and February. In late February or early March, the number of grouse found in flocks declined as older males returned to breeding areas. For example, 54% of 406 males were found in aggregations between 1 October and 1 March but only 18% of 160 males sighted in March were in groups (contingency table, $P < 0.01$). In April, 22% of the males ($N = 373$) and 36% of the females ($N = 148$) sighted during census of the main study area were with other grouse. The latter figure likely over-estimated the proportion of females in groups because the census crew concentrated on territorial males early in spring and many of the females recorded were with these males. In April 1982, I intensively searched a 50-ha plot as part of a study of movements and spatial relationships of female grouse and found 10 (18%) of 57 females with other grouse. This is probably a better indicator of the gregariousness of females during April.

Seasonal trends in flock size followed a similar pattern to the above data (Figure 4.2). Flocks were relatively small in November but increased in size until January and then declined. Flocks sighted after brood break-up (>1 October) consisted of 2 to 15 birds and averaged 2.9 ± SE 1.9 ($N = 210$). Two was by far the most common group size (Figure 4.3).

The tendency to join flocks varied somewhat among sex-age classes. From 1 October (after the end of brood break-up) until the time of spring migration (beginning approximately 1 March for males, and 1 April for females), 46% of 127 adult males, 38% of 112 adult females, 57% of 170 juvenile males, and 55% of 267 juvenile females were in groups. The proportion of grouse found in groups differed among sex-age classes (contingency table, $P < 0.01$); the only significant pairwise contrast ($P < 0.05$) indicated that adult females were less apt to be found in groups than were juvenile males or females.

Overall, 54% of the males ($N = 406$) and 51% of the females ($N = 495$) observed between the time of brood break-up and spring migration were in groups (grouse of known sex but unknown age were also included in these samples). If data for both sexes are pooled, and observations of birds of unknown sex are added to the sample, an estimated 52% of the grouse were in groups (N = 1029).

4.3.3 Associations among Different Sex and Age Classes

Grouse associated most frequently with individuals of their own sex and age (although some degree of association between all sex-age classes was found). For example, 68% of all adult males found in groups were associated with at least one other adult male whereas only 15% were associated with adult females, 24% with juvenile males, and 9% with juvenile females (Table 4.1). Adult females showed lesser tendencies to flock with members of their own sex and age than did any of the other sex-age classes.

4.3.4 Daily Movements and Home Range Size

Daily movements of radio-marked grouse were highest in late summer but decreased throughout fall and remained low but stable throughout winter (Figure 4.4). Daily movements varied from 0 to over 600 m but the median for the period lasting from 1 October until spring migration was only 69 m indicating that short daily movements were typical (Figure 4.5).

Sizes of winter home ranges were measured for 18 radio-marked juvenile females, 2 juvenile males, and 1 adult female. Home ranges during winter varied in size from 3.0 to 42.5 ha and averaged 16.8 ± 2.3 ha (N = 21). In many instances, overlap of home ranges was substantial (Figure 4.6). Only radio-marked grouse on part of the island are shown in Figure 4.6 and, as many other grouse resided in this area, home range overlap was undoubtedly more extensive than indicated on the map.

4.4 Discussion

Winter was a time of relatively low mobility for blue grouse on Hardwicke Island. Daily movements <100 m were most frequent and home ranges averaged 16.8 ha for a 4 to 5 month period. Grouse were most often found alone or in small groups of 2 or 3 in late fall and winter. The data suggest that winter associations of juveniles were comprised of non-siblings.

Immediately after brood break-up, the tendency to form flocks was low but the rates of aggregation gradually increased until mid-winter then declined until spring. Similar trends in winter flocking are shown by ruffed grouse (*Bonasa umbellus*) (Doerr et al. 1974), black grouse (*Tetrao tetrix*) (Hanson and Soikkeli 1984), and capercaillie (*Tetrao urogallus*) (Pulliainen 1981). Doerr et al. (1974) suggested that decreases in feeding aggregations of ruffed grouse from January through March came about when males became socially intolerant of each other or more attached to their territories. This was likely true for blue grouse on Hardwicke Island as there were proportionally fewer males in late winter flocks than in earlier groupings. Final dissolution of winter flocks occurred when females returned to breeding range.

Although blue grouse associated most frequently with individuals of their own sex and age, they did not show as a strong a tendency to segregate by sex as found in some other species of grouse. Studies of migration (Hines 1986*a*) and winter habitat use by blue grouse (Hines 1986*b*) suggest 2 factors that may have contributed to the partial segregation by sex and age. First, juveniles wintered farther from breeding range than did adults thereby bringing about segregation of the age classes (Hines 1986*a*). Second, females wintered at lower elevations than did males and the 2 sexes were separated somewhat because of this (Hines 1986*b*). Given that both migration distances and the elevations that the different sex and age classes wintered at were somewhat variable, the segregation of sex and age classes was incomplete. Data for other species of North American grouse support the view that segregation of the sexes is influenced by migration (Table 4.2). Segregation occurs most frequently when one sex winters closer to the breeding range (e.g., sage grouse, white-tailed ptarmigan, sharp-tailed grouse) and formation of mixed flocks is more common in species which show little evidence of differential migration of the sexes (e.g., blue grouse on Hardwicke Island, spruce grouse in Alaska, ruffed grouse).

The question of why certain sex-age classes associated with each other was considered above but this does not explain why there is such a range in gregariousness among species. To address the latter point, data on fall and winter groupings of blue grouse and other North American Tetraoninae were summarized with regard to typical and maximum flock size, and winter habitat (Table 4.2). Although not all information was available for each species, a general trend seemed apparent: species wintering in more open habitats form larger flocks (e.g., sage grouse, white-tailed ptarmigan, sharp-tailed grouse) whereas species wintering in forested areas live solitarily or in small groups (e.g., ruffed grouse, blue grouse, spruce grouse).

Why are species that winter in open habitats more gregarious? There are at least 3 ultimate or evolutionary pressures on animals to live in groups during the non-breeding season (Alexander 1974, Wilson 1975, Pulliam and Millikan 1982, Madison 1984). By joining a group, an individual might (1) increase its chance of avoiding predators or (2) find and exploit a food resource more efficiently. Further, animals might aggregate in certain areas because (3) resources essential for survival are clumped in distribution and not easily defended (Pulliam and Millikan 1982). The literature on grouse provides little information about point (3) -- it is not known if essential resources are more clumped in open than forested areas. To my knowledge, instances of starvation have seldom been reported for grouse (e.g., McGowan 1969) suggesting that the need to optimally exploit a food resource (point 2) may not be a selective pressure on tetraonine sociality. Predation is a frequent cause of death for Tetraonines (Jenkins et al. 1964, Gullion and Marshall 1968, Rusch and Keith 1971), thus it is possible that flocking is an anti-predator response used by grouse inhabiting open areas (but less useful to those living in forests). Comparisons of the distribution and abundance of resources, and assessments of the relative merits of flocking for maximizing feeding or avoiding predators in open versus forested habitats (and the synergistic interactions between these variables) are needed to resolve this issue.

4.5 Summary

Social organization, movements, and home ranges of wintering blue grouse were investigated from 1979 to 1982. Most broods had disbanded by the end of September and young grouse did not associate with their mothers or siblings in winter. The tendency to form flocks was lowest in fall but sociability gradually increased until mid-winter and then declined until spring. Approximately half of the grouse sighted during winter were in groups which usually consisted of 2 or 3 birds and averaged 2.9 ± SE 1.9 ($N = 210$). Daily movements were usually small in winter (median = 69 m) and home ranges averaged 16.8 ± 2.3 ($N = 21$). Although blue grouse did not show the strong segregation of sexes found in some other tetraonines, birds most frequently associated with individuals of their own sex and age. The partial segregation by sex and age may have resulted because females wintered at lower elevations than males and juveniles migrated longer distances than adults. Segregation of sexes of other Tetraoninae may be explained by a similar mechanism. Flock formation is most frequent

among species of grouse that winter in open areas and less frequent among species that winter in forests. The possible reasons for these differences are discussed.

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TABLE 4.1. Associations between blue grouse of different sex and age on Hardwicke Island, British Columbia, 1 October to 31 March. Data include only grouse seen in flocks.

		Percent in flocks with			
Age - sex	Number seen in flocks	Adult males	Adult females	Juvenile males	Juvenile females
Adult males	66	68.2	15.2	24.2	9.1
Adult females	43	23.3	23.3	18.6	30.2
Juvenile males	98	15.3	16.3	73.5	50.0
Juvenile females	148	6.8	12.2	28.4	73.7
		Other males		Other females	
Males (all ages)[a]	247	80.6		53.4	
Females (all ages)[a]	251	41.0		76.1	

[a] Analysis includes 83 males and 60 females of unknown age.

TABLE 4.2. Factors associated with flocking in North American grouse.

Species	Location	Lone grouse	Typical or mean flock size	Maximum flock size	Segregation of sexes	Winter habitat	Differential migration of sexes	Source
Sage grouse	Colorado	infrequent	<50	100+	yes	sagebrush-grassland	yes	Beck (1977)
White-tailed ptarmigan	Colorado	infrequent	<25	80+	yes	alpine willow	yes	Hoffman and Braun (1975, 1977)
Willow ptarmigan	Alaska	infrequent	?	?	yes	willow	yes	Weeden (1964), Irving et al. (1967)
Rock ptarmigan	Alaska	infrequent	<20	100	yes	willow	yes	Weeden (1964)
Spruce grouse	Alaska	frequent	2 - 4	15	no	coniferous forest	no?	Ellison (1973)
Sharp-tailed grouse	Saskatchewan	?	5 - 10	?	yes	aspen parkland	yes	Schmidt (1980)
Sharp-tailed grouse	Wisconsin	?	?	200	yes	brushy areas	yes	Hamerstrom and Hamerstrom (1951)
Blue grouse	Colorado	frequent	3 - 6	20	moderate	coniferous forest	yes	Cade (1985)
Blue grouse	British Columbia	frequent	2	4	yes	coniferous forest	yes	King (1971)
Blue grouse	British Columbia	frequent	2 - 3	15	moderate	coniferous forest	no	this study
Sage grouse	Idaho	?	<50	300	yes	sagebrush	?	Dalke et al. (1963)
Ruffed grouse	Alberta	frequent	2 - 3	9	no	aspen forest	no?	Doerr et al. (1974)
Ruffed grouse	Saskatchewan	frequent	2	8	?	deciduous forest	?	Hines (1984)

FIGURE 4.1. The proportion of juvenile blue grouse with adult females during fall and winter on Hardwicke Island, British Columbia. Sample sizes are indicated for each interval.

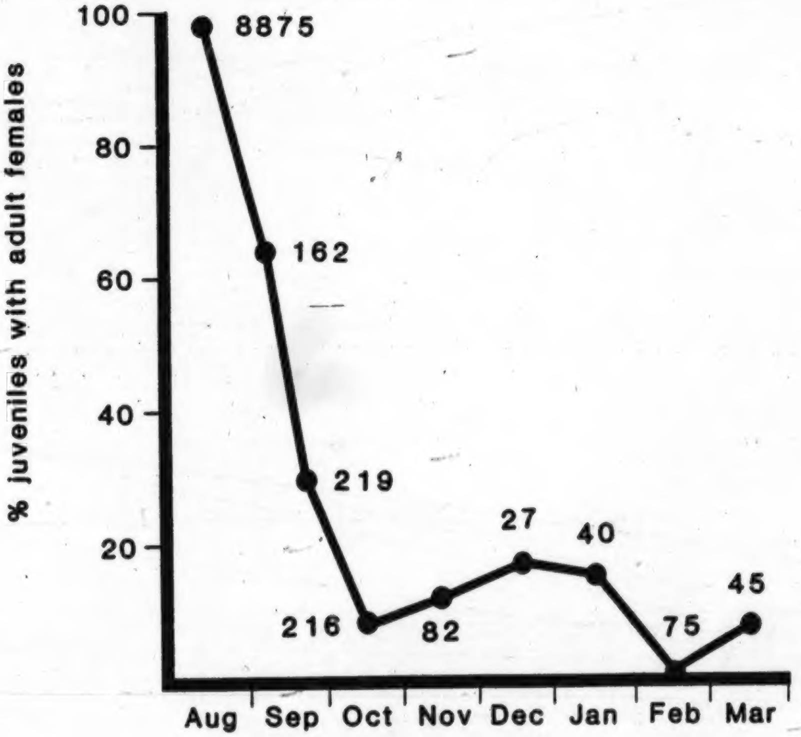
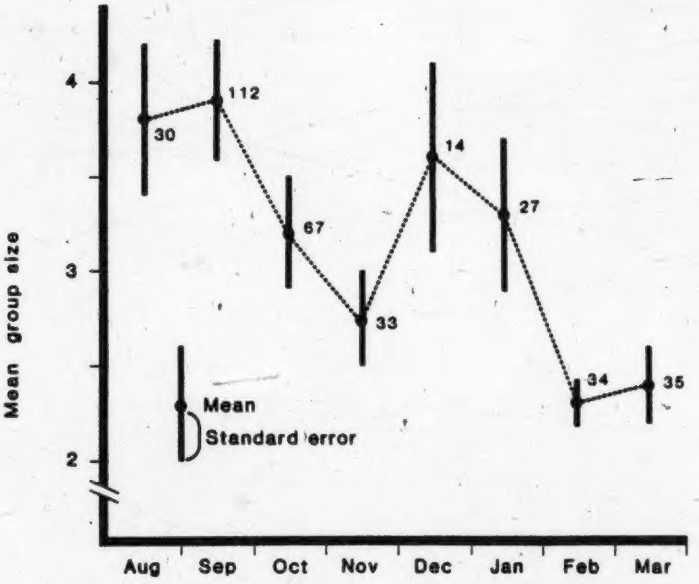

% juveniles with adult females
100
80
60
40
20
8875
162
219
216
82
27
40
75
45
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar

FIGURE 4.2. The average size of flocks during fall and winter and the proportion of all grouse found in flocks. Sample sizes are indicated for each interval.


Mean group size
4
3
2
30
112
67
33
14
27
34
35
Mean
Standard error
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar

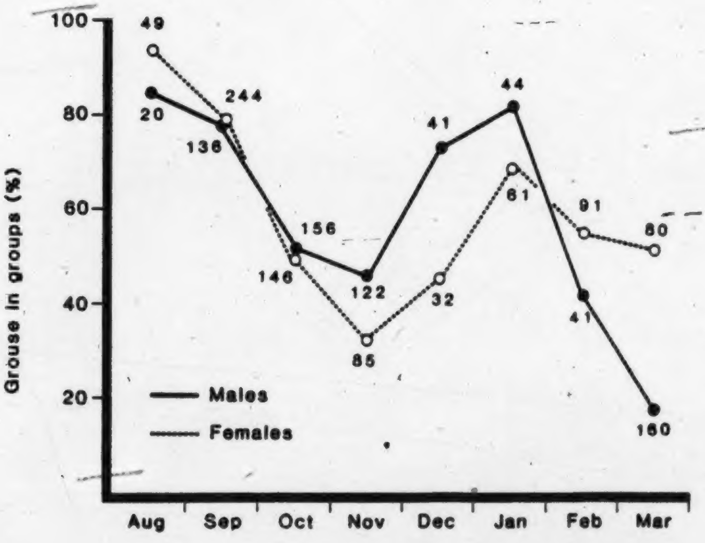

Grouse in groups (%)
100
80
60
40
20
49
20
244
136
156
146
122
85
41
32
44
61
91
41
80
160
Males
Females
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar

FIGURE 4.3. Flock sizes of blue grouse sighted between 1 October and the time of spring migration. The number of flocks of each size is indicated above the histogram.

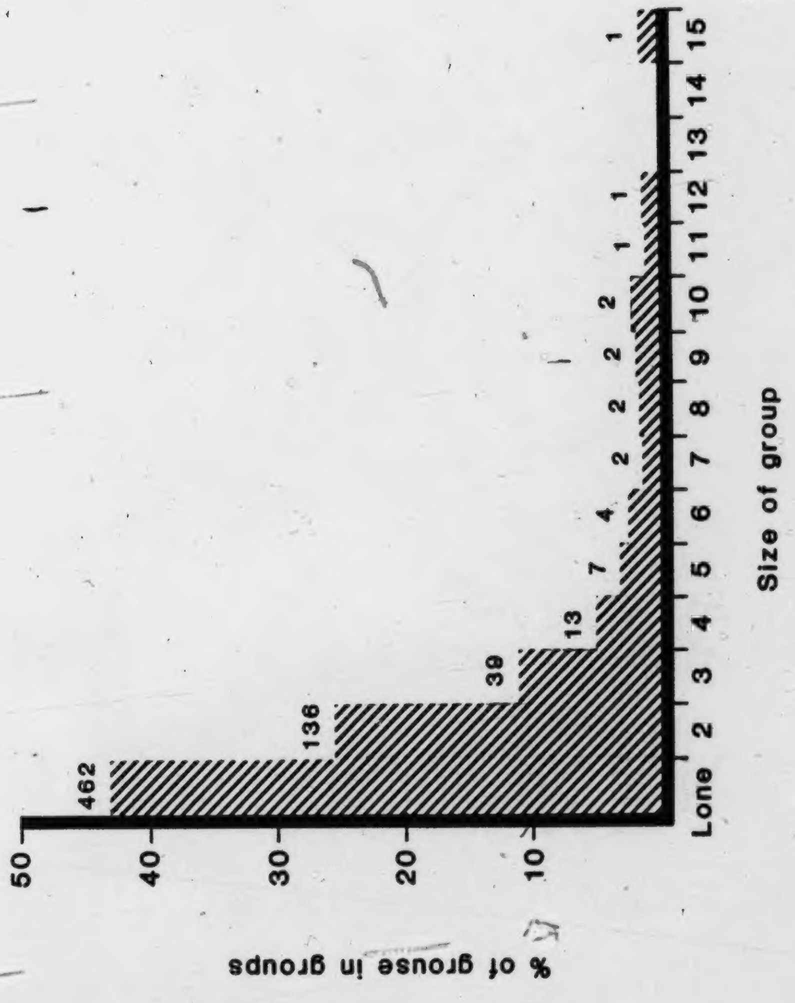

% of grouse in groups
50
40
30
20
10
Size of group
Lone
2
3
4
5
6
7
8
9
10
11
12
13
14
15
462
136
39
13
7
4
2
2
2
2
1
1
1

FIGURE 4.4. Seasonal changes in daily movements (m) of radio-marked blue grouse. Sample sizes are indicated for each interval.

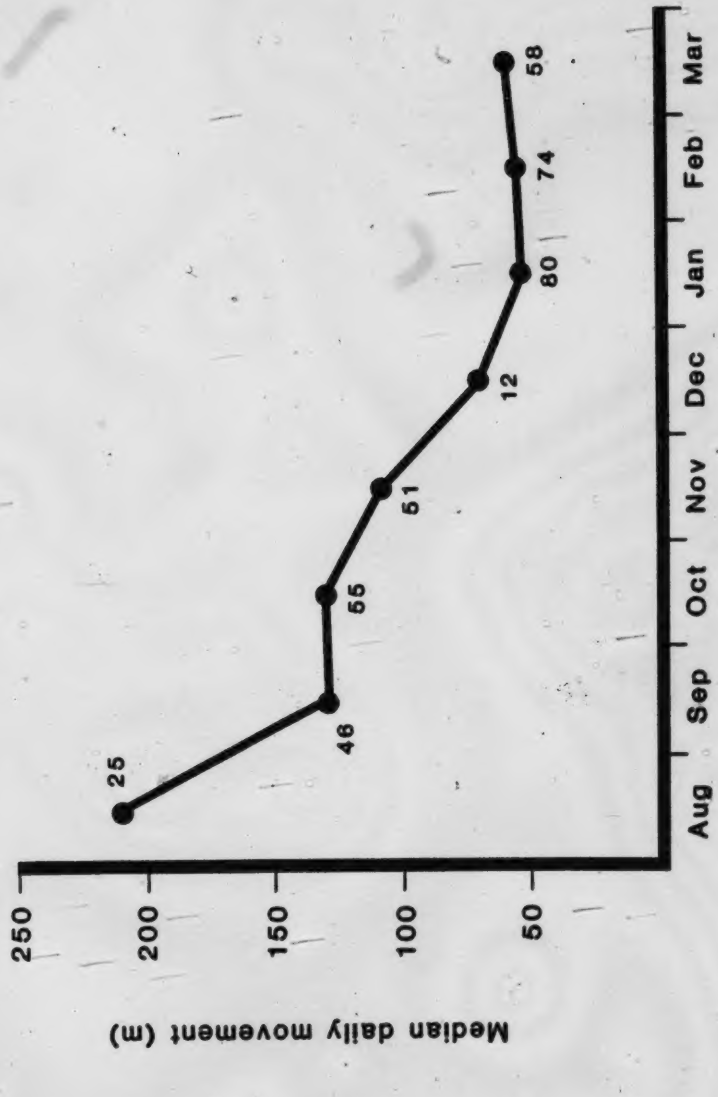

Median daily movement (m)
250
200
150
100
50
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
25
46
55
51
12
80
74
58

FIGURE 4.5. Daily movements (m) of radio-marked blue grouse during fall and winter. Sample sizes are indicated above the histogram.

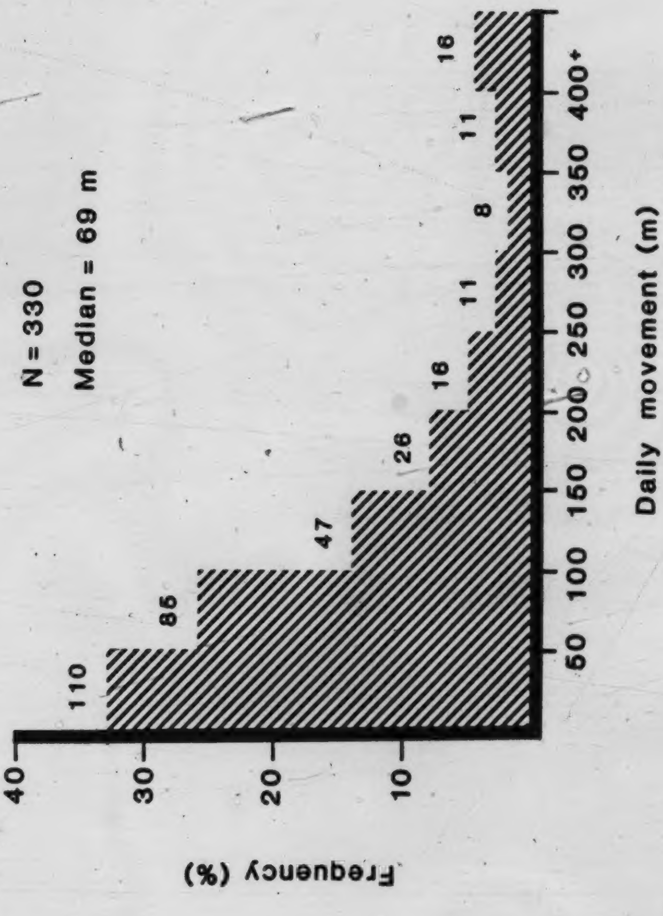
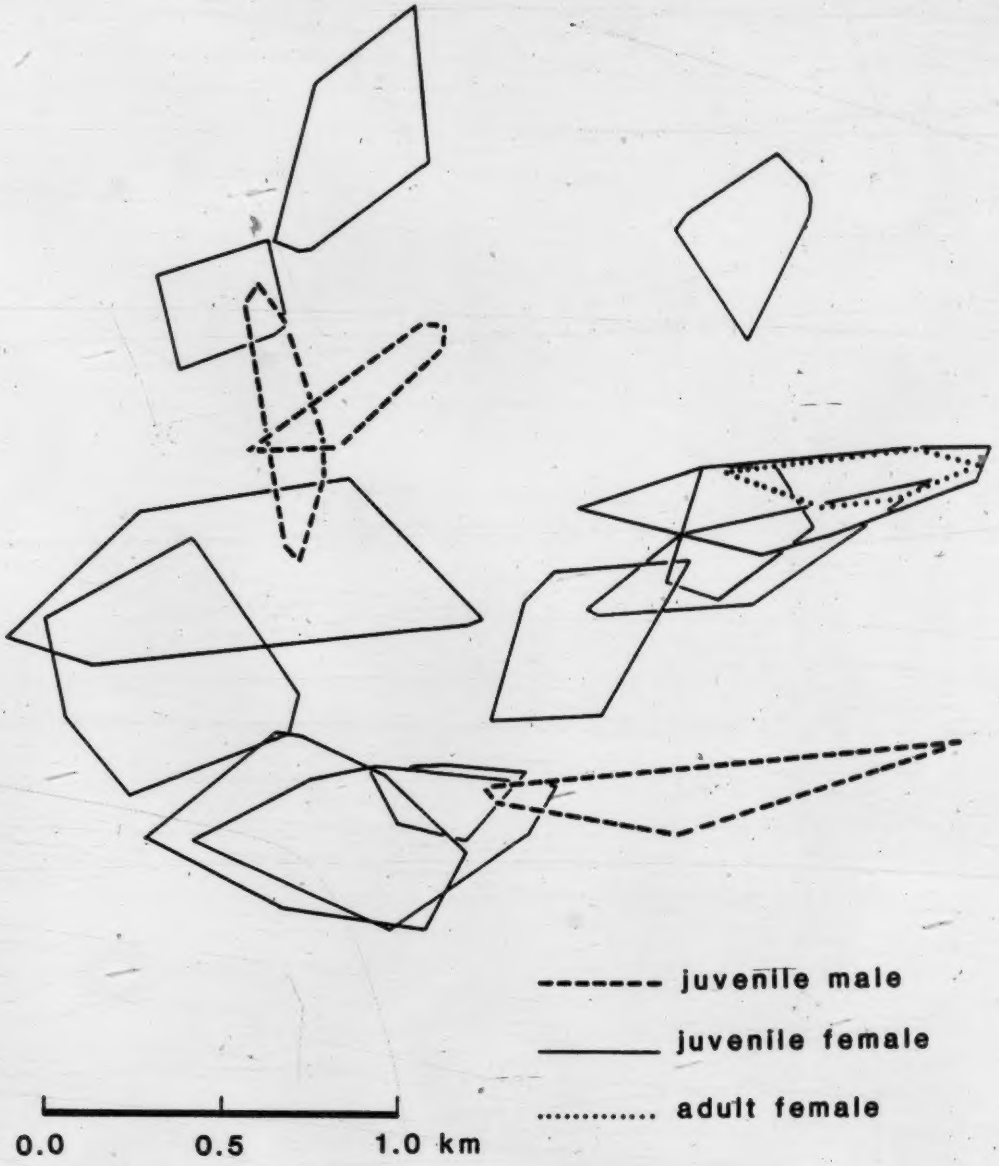

N = 330
Median = 69 m
Frequency (%)
40
30
20
10
110
85
47
26
16
11
8
11
16
50
100
150
200
250
300
350
400+
Daily movement (m)

FIGURE 4.6. Overlap of home ranges of radio-marked blue grouse on part of Hardwicke Island, British Columbia during the winter of 1981-1982.


juvenile male
juvenile female
adult female
0.0
0.5
1.0 km

5. SURVIVAL AND REPRODUCTION OF DISPERSING BLUE GROUSE

5.1 Introduction

Dispersal, the movement between place of birth and place of breeding, or where an animal settled and would have bred had it not died (Howard 1960), has important implications for limitation or regulation of populations (Lidicker 1975, Watson and Moss 1979, Tamarin 1983, and others). Hypothetically, as population density increases, social interactions might become more intense causing increased rates of emigration with dispersers having relatively poor survival and reproductive success (Christian 1970, Lidicker 1975, Krebs 1978, Moss et al. 1982, Tamarin 1983). As a consequence, population growth could be limited by increased dispersal at higher densities and the relatively low fitness of dispersing animals.

Despite these arguments, there seems to be little published evidence that dispersal is greatly influenced by population density. In a critical review of dispersal in small mammals, Gaines and McClenaghan (1980:189) wrote: "In species for which adequate demographic data are available, dispersal is clearly a density-independent phenomenon", a conclusion reached also by Stenseth (1983). Although Greenwood and Harvey (1982), in their review on dispersal in birds, suggested that the effects of density on dispersal were well established, I have been able to find little evidence that this is so from the literature. Most evidence is based on disappearance of animals from particular study areas and many authors have equated "disappearance" with dispersal despite the fact that dead animals are usually difficult to find and disappearance may represent *in situ* mortality (Gaines and McClenaghan 1980).

The idea that dispersers fare poorly especially stems from the work of Errington (1946, 1963) who suggested that young, wandering muskrats (*Ondatra* *zibethicus*) were particularly susceptible to predation. Various workers have implied that this was true for other species but supporting data are scarce. For small mammals, Gaines and McClenaghan (1980:190) observed: "As far as we know, with the exception of some anecdotal information, there are no data on survival and reproduction of individuals after they leave a resident population." Similarly, Greenwood and Harvey (1982) noted that the life history consequences of avian dispersal were largely unknown.

As part of a population study of blue grouse (*Dendragapus obscurus*), on Hardwicke Island, British Columbia, 293 juveniles were equipped with radio transmitters in late summer and fall, 1979-1982. I was able to follow many of these grouse to their eventual fate and distinguish between death and dispersal. For females, I was able to determine reproductive success. Supplementary data on other juveniles (which were banded or wing-tagged but not radio-marked) were collected also. In this paper, I analyse distances moved by male and female grouse, evaluate the effects of changing population density on dispersal distance, and consider the relative survival and reproductive success of short- and long-distance dispersers.

5.2 Study Area and Methods

The study area, Hardwicke Island (50° 28' N, 125° 50' W), lies between Vancouver Island and the mainland of British Columbia, Canada. The area of the island is 77 km^2; 465 ha comprise the main study area for blue grouse research. Roughly one fourth of the island and over 90% of the main study area has been logged during the past 20 years. These "clearcuts" support the highest densities of blue grouse during the breeding season whereas other successional stages, 21 to over 250 years in age, support only sparse densities (Niederleitner 1982).

General methods used in the study of blue grouse populations have been described by Zwickel and Bendell (1967*a*) and Zwickel (1982). Adults, yearlings, and large juveniles are captured with noosing poles (Zwickel and Bendell 1967*b*) and color-banded for future identification. Smaller chicks (<4 weeks old) are usually caught by hand and marked with numbered, patagial wing-tags. A minimum estimate of adult and yearling female numbers is the number of different females identified on the study area annually. Usually about 80% of the adult males on the study area are color-banded and their territories, plus those of unbanded or unidentified individuals are plotted on maps to calculate total numbers of territorial males. Production of young (the number of juveniles present on the study area in late summer) is calculated by multiplying the number of females seen with broods by average brood size for August. During late summer and fall, juvenile blue grouse were equipped with radio transmitters mounted as back-pack units similar to those described by Brander (1968). Radio packages weighed from 2 to 6% of the body weight of juveniles at this time and had little obvious effect on survival, reproduction, or movements of grouse (Hines and Zwickel 1985). Numbers of grouse radio-marked were 60 in 1979, 97 in 1980, 78 in 1981, and 58 in 1982, for a total of 293. Mortality of young grouse was high and only 24 males and 42 females provided information on dispersal. Sample sizes available for different analyses vary somewhat because of radio failure or deaths of radio-marked grouse after dispersal had been completed.

Data on dispersal came from: 1) grouse that were wing-tagged or leg-banded as juveniles and later recaptured or reobserved as yearlings or adults, and 2) grouse that were equipped with radios as juveniles. Dispersal distance was defined as the straight line distance between location of birth and location of settlement as a yearling. Actual location of birth was known for only a small proportion of all grouse that hatched on the study area and, for most juveniles, I used earliest location in summer as an approximation of site of birth. This was thought to be valid because, during June and July when most juveniles were first captured, broods were an average distance of 320 ± SE 29 m from their place of hatch (based on 115 sightings of 48 females whose nest location was known). Nest site, if known, was used as place of breeding for yearling females. For males, and females for which no nest was found, mean location during spring (before 15 June) was used to estimate site of breeding.

For analytical purposes, I defined "long-dispersers" as animals moving greater than the median dispersal distance and "short-dispersers" as those moving less than the median distance. Non-radioed individuals, which disperse long distances and leave the study area, are not apt to be found by normal census procedures and the median dispersal distance for this group is likely underestimated. Therefore, median dispersal distance as measured for radioed grouse, was used to separate long- from short-dispersers among non-radioed birds.

All blue grouse disperse to some degree, but to make the data more directly comparable to other studies where dispersal is viewed as a black and white process (i.e., animals either disperse or do not disperse), the following analysis was undertaken. "Dispersers" were defined as those individuals settling off the main study area and "non-dispersers" were those grouse that settled on the main study area. The data were then examined to determine if "dispersal" influenced survival or reproductive success. Grouse marked off the main study area were omitted from this analysis.

Evidence of nesting was used as an indicator of reproduction for radio-marked females. Survival during the reproductive period (1 April to 15 June) was also compared for long- and short-dispersers. I considered non-radioed females to have bred if they were seen with a brood, or if they had a brood patch (an indicator of incubation). Survival during spring could not be evaluated for non-radioed grouse.

Data on dispersal distances were tested for normality using a Kolmogorov-Smirnov test for goodness-of-fit and transformed via logarithms if the distribution was not normal. The normalized data were tested with a 2-way ANOVA to see if dispersal distances differed between sexes or among years. Survival rates and indicators of reproductive success were compared using Fisher's exact test (when sample sizes were less than 50) or X^2 contingency tables (when sample sizes were larger).

5.3 Results

5.3.1 Dispersal Distances

After log-transformation to normalize the data, a 2-way ANOVA showed that dispersal distances differed between sexes ($P = 0.01$) but not among years ($P = 0.44$, Table 5.1). Subsequently, I pooled the data for all 4 years and obtained a median dispersal distance of 0.9 km for males and 1.4 km for females (Figure 5.1).

For leg-banded or wing-tagged individuals that were not equipped with radios, data were normally distributed without transformation. A 2-way ANOVA indicated no significant differences among years ($P = 0.49$) although there was a significant difference between sexes ($P = 0.02$, Table 5.2). The distribution of dispersal distances was similar in appearance for radio-marked and non-radioed birds (Figure 5.2) but distances for females in the latter group were shorter than for the former (Mann-Whitney U-test, $P = 0.03$). This was likely an artifact of sampling procedures as few non-radioed animals that dispersed beyond the boundary of the study area were found by census crews. Although the trend was in the same direction, the two samples of males did not differ significantly ($P = 0.11$), possibly because of small sample sizes in the radio-marked group.

5.3.2 Influence of Population Density on Dispersal

The number of territorial males on the main study area was 152 in 1980, 140 in 1981, 123 in 1982, and 94 in 1983. Numbers of banded adult plus yearling females were 276, 208, 162, and 113 in these years. Production of young decreased steadily from an estimated 847 in 1979 to 612 in 1980, 354 in 1981, and 224 in 1982. To find if changes in population density had any influence on dispersal, I used a regression analysis with dispersal distances (for each individual) as dependent variables and densities of adult males, adult females or juveniles (in the previous fall) as independent variables. Samples of radio-marked or non-radioed grouse were considered separately in this analysis. For both samples, dispersal distances of yearling females were not correlated with density of females in spring (for radio-marked females, $r = 0.02$, $N = 42$, $P = 0.91$; for non-radioed females, $r = -0.08$, $N = 70$, $P = 0.51$) or density of juveniles in the previous fall (for radio-marked females, $r = 0.02$, $N = 42$, $P = 0.90$; for non-radioed females, $r = -0.08$, $N = 70$, $P = 0.48$). Radio-marked males appeared to disperse shorter distances in years of low adult density ($r = 0.38$, $N = 24$, $P = 0.07$) or following years of low production of juveniles ($r = 0.40$, $N = 24$, $P = 0.05$). This relationship did not hold for the sample of non-radioed males as there was little correlation between dispersal distance and density of adult males ($r = 0.14$, $N = 56$, $P = 0.30$) or density of juveniles ($r = 0.11$, $N = 56$, $P = 0.44$).

One might argue that although median dispersal distances were relatively constant among years, the proportion of grouse dispersing varied annually. The proportion of grouse dispersing long distances was 10 of 13 in 1979-1980, 7 of 16 in 1980-1981, and 10 of 24 in 1981-1982, and 6 of 13 in 1982-1983 (samples of males and females were pooled because of small sample sizes). The proportion of grouse dispersing longer distances did not vary among years (X^2 contingency table, $P = 0.19$).

5.3.3 Survival and Reproduction of Long- and Short-distance Dispersers

Among radio-marked grouse, long-dispersers of both sexes survived as well as short-dispersers during spring (Table 5.3). Reproductive success of females also seemed equivalent between groups as the proportion of females alive on 1 April that eventually nested and the proportion of females that survived the reproductive period and nested, were similar for both samples (Table 5.3, $P > 0.10$ in all instances).

Blue grouse prefer early successional stages for breeding (Niederleitner 1982) and one might expect that long-dispersers, if they are socially subordinate, would be more apt to settle in poorer quality (older) habitats than short-dispersers. Although 6 long-dispersing females settled in more mature habitats (>20 years in age), the median age of habitats occupied by 32 long-dispersers was 10 years (range 3 - 250+) and did not differ significantly from that for short-dispersers (median = 11 years, range 3 - 20, Mann-Whitney U-test, $N = 32$, $P = 0.45$). I conclude that long-dispersers found early successional habitats as well as did short-dispersers.

I could not directly assess the proportion of non-radioed yearling females that bred because their nests were difficult to find. For this group, females sighted with broods or captured females which had brood patches were considered to be breeders. Nearly equal percentages of long-dispersing (75% of 24) and short-dispersing (74% of 42) females showed signs of breeding, indicating that dispersal did not influence reproductive success (X^2 contingency table, $P = 0.92$).

Another possible indicator of fitness is time of nesting. For a pooled sample of radio-marked and non-radioed grouse, mean date of hatch was similar for the broods of long- (16 June ± SE 2 days, $N = 21$) and short- (17 June ± 1 day, $N = 27$) dispersers (Mann-Whitney U-test, $P = 0.57$). I conclude that the act of dispersing a longer distance did not delay nesting in females.

A commonly used operational definition of a disperser is an animal which settles off the study area. For radio-marked grouse originating from the main study area, the survival and reproductive success of birds settling either on (non-dispersing) or off the study area (dispersing) were compared. Neither survival nor reproductive status differed between groups (Table 5.4).

5.4 Discussion

The hypothesized role of dispersal in limiting or regulating populations rests on two important tenets: (1) dispersal varies annually or with changes in population density, and (2) dispersers have relatively poor survival and reproductive success. The implications of my results with regard to these assumptions are now considered.

Data for both radio-marked and non-radioed grouse demonstrate that annual changes in population density had little effect on the distance dispersed by young females. This occurred despite the fact that spring density of female grouse on the main study area decreased by about 60% and numbers of juveniles decreased by a factor of about 4 during the study. For males, the data are inconclusive. Radio-marked males apparently moved farther in years following high production of chicks and when densities of adult males were high. The sample of non-radioed grouse indicated no such correlation and the overall relationship between population density and dispersal distances of males is unclear.

To my knowledge, few studies of birds have shown that dispersal is greatly influenced by population density, despite the claim of Greenwood and Harvey (1982) to the contrary. In an earlier paper (Greenwood et al. 1979), these authors reported that dispersal was inversely correlated with population density in female great tits (*Parus major*) while it was positively correlated with density in males. They used two criteria for measuring dispersal; distance and the number of territories between place of birth and place of settlement after dispersal. Dispersal distance was inversely correlated with population density in females and there was no significant correlation between male density and dispersal distance. They indicated a positive relationship between number of territories dispersed and population density for males only. This correlation was of borderline significance ($0.05 < P < 0.10$) and could be spurious. If dispersal distances were constant between years, birds would necessarily move across more territories in years of high density than in years of low density. Other studies, relating dispersal in great tits to population density, equate disappearance of animals with dispersal (Dhondt 1971, Kluyver 1971) but such disappearing animals may have died rather than dispersed. Jenkins et al. (1964) reported that numbers of dispersing red grouse (*Lagopus lagopus scoticus*) were greatest in years of high population density and lowest in years of population lows. They did not show that *rates of dispersal* increased with density and my calculations, based on their Table 5, revealed no correlation between proportion of animals that dispersed and population size ($r = 0.10$, 7 df, $P = 0.80$). More recently, Watson et al. (1984) reported that spring dispersal was density dependent in red grouse.

If dispersal of blue grouse is not greatly influenced by population density, perhaps it is "innate" (Howard 1960) or has a large "presaturation" component (Lidicker 1975). Several authorities have suggested that this might be the case among other birds. For example, Weise and Meyer (1979) believed that dispersal of black-capped chickadees (*Parus atricapillus*), which occurred mainly in late summer when aggression was low, was largely innate. Similarly, Alway and Boag (1979) found minimal aggression associated with fall movements of spruce grouse (*Dendragapus canadensis*) although they reported greater aggression at the time of spring dispersal. For the same species, Keppie (1979) demonstrated that although dispersal was important in determining the size of the population on his study area, it was not density dependent.

Although sample sizes are small, my data suggest that dispersing females were able to settle and breed as soon as short-dispersers and that the act of dispersing did not greatly influence subsequent reproduction or survival in spring. However, a potential bias arises because dispersal distance is influenced by a complex interaction of movements including fall migration to winter range, spring migration to potential breeding habitats, and, to a lesser degree, movements on breeding range (Hines 1986). As a result, I could not determine which grouse were long-dispersers and which ones were short-dispersers until they arrived on breeding range. If long-distance or short-distance dispersers suffered different rates of mortality before arriving on breeding range in spring, the effect of dispersal on survival would be estimated inaccurately. About two-thirds of the over-winter mortality of radio-marked grouse occurred before juveniles migrated in fall or after they had localized on winter range, thus most losses were not associated with the time of year when grouse moved widely and were not directly attributable to dispersal.

Overall, my data do not support the viewpoint that dispersers fare poorly. Similar information on the fate of dispersing individuals are sparse in the literature. For great tits, there is some evidence that dispersers survive (Dhondt 1979, Greenwood et al. 1979) and reproduce (Greenwood et al. 1979) as well as do non-dispersers. In contrast, Jenkins et al. (1964) suggested that juvenile mortality was highest at the time of year when young red grouse dispersed and implied that this relationship was cause and effect. Mortality of adult grouse (which do not disperse) was also greatest at this time of year (Jenkins et al. 1963, Table 27) indicating that high mortality was not necessarily caused by dispersal.

Several authors have implicated dispersal as an important factor in limiting populations of birds and mammals (Krebs and Myers 1974, Watson and Moss 1979, Tamarin 1983). Dispersal distances for female blue grouse were relatively constant from year to year and had little influence on subsequent survival or reproductive success. Accordingly, it would be difficult to argue that annual variations in dispersal greatly influenced recruitment to this population.

The present study covered only a 4-year period, at a time when population levels declined greatly, and results may not be representative of what would occur in increasing or more stable populations of blue grouse or other animals. Despite this shortcoming, my data indicate that for blue grouse, the act of dispersing was not necessarily a liability. Long-distance dispersers found suitable habitats, settled, and maintained high rates of reproduction and survival. Perhaps, for blue grouse and many other species, dispersal should be viewed as an essential feature of the life history of an individual rather than a fate suffered by "doomed" individuals.

5.5 Summary

Dispersal in a declining population of blue grouse was studied from 1979 to 1983 by radio-tracking 66 individuals and reobserving or recapturing 126 color-banded individuals. On a 465-ha main study area, numbers of territorial males decreased from 152 to 94, breeding females from 276 to 113, and young grouse alive in late summer from 847 to 224 during the period of study. Despite this, dispersal distances did not vary between years and there was no clear relationship with adult densities in spring or density of juveniles in the previous fall. Rates of survival and reproduction for "long-dispersers" (grouse moving greater than the median dispersal distance) and "short-dispersers" (grouse moving less than the median dispersal distance) were similar. Similar results were noted for grouse that left the study area ("dispersers") and those that remained on the study area ("non-dispersers"). Overall, there was little evidence that dispersers fared poorly or that dispersal was greatly influenced by population density.

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TABLE 5.1. Dispersal distances (km) of radio-marked blue grouse, 1979-1983.

	Males			Females		
Year	Median	*N*	Range	Median	*N*	Range
1979 - 1980	1.4	6	0.9 - 2.6	1.5	7	0.3 - 10.8
1980 - 1981	0.9	7	0.3 - 1.8	1.3	9	0.3 - 3.3
1981 - 1982	0.9	6	0.2 - 1.9	1.1	18	0.4 - 11.0
1982 - 1983	0.7	5	0.5 - 1.7	2.2	8	0.3 - 5.7
All years	0.9	24	0.2 - 2.6	1.4	42	0.3 - 11.0

TABLE 5.2. Dispersal distances (km) of non-radioed blue grouse, 1979-1983.

	Males			Females		
Year	Median	*N*	Range	Median	*N*	Range
1979 - 1980	0.7	18	0.2 - 1.7	1.0	29	0.2 - 2.7
1980 - 1981	0.8	14	0.3 - 2.1	1.0	27	0.1 - 2.2
1981 - 1982	0.8	19	0.1 - 1.4	1.3	12	0.1 - 2.4
1982 - 1983	0.5	5	0.1 - 1.1	1.1	2	0.8 - 1.4
All years	0.7	56	0.1 - 2.1	1.1	70	0.1 - 2.7

TABLE 5.3. Survival through the breeding season (1 April to 15 June) and reproduction by short- and long-dispersers, 1979-1983. Sample sizes are in parentheses.

Parameter	Short-dispersers[a]	Long-dispersers[b]	*P*[c]
Percent survival (males)	82 (11)	75 (12)	1.00
Percent survival (females)	74 (19)	75 (20)	1.00
Percent of all females nesting	68 (19)	50 (20)	0.33
Percent of females surviving breeding season that nested	93 (14)	67 (15)	0.17

[a] Grouse dispersing <0.9 km for males, <1.4 km for females.

[b] Grouse dispersing >0.9 km for males, >1.4 km for females.

[c] Fisher's exact test.

TABLE 5.4. Survival through the breeding season and reproduction by radio-marked grouse settling on ("non-dispersers") and off ("dispersers") the main study area, 1979-1983. Sample sizes are in parentheses.

Parameter	"Non-dispersers"	"Dispersers"	P[a]
Percent survival (males)	81 (16)	71 (7)	1.00
Percent survival (females)	74 (23)	73 (15)	1.00
Percent of all females nesting	61 (23)	53 (15)	0.74
Percent of females surviving breeding season that nested	82 (17)	73 (11)	0.65

[a] Fisher's exact test.

FIGURE 5.1. Dispersal distances (km) for radio-marked blue grouse, 1979-1983. Sample sizes are indicated above the histogram.

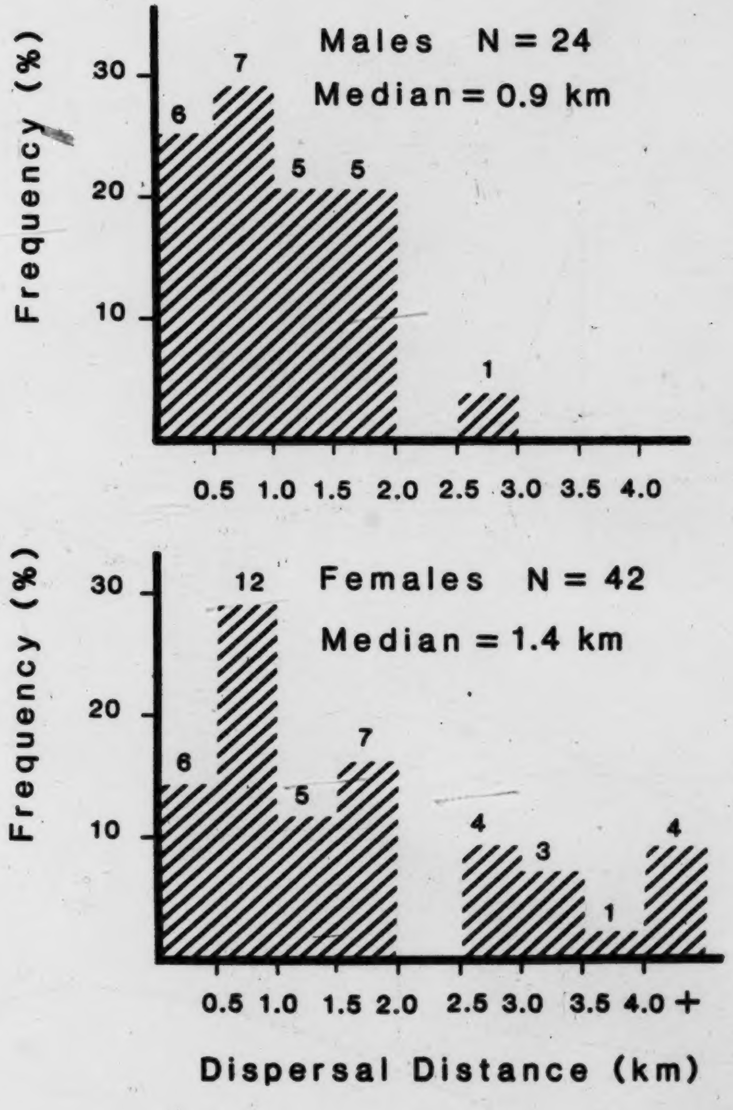
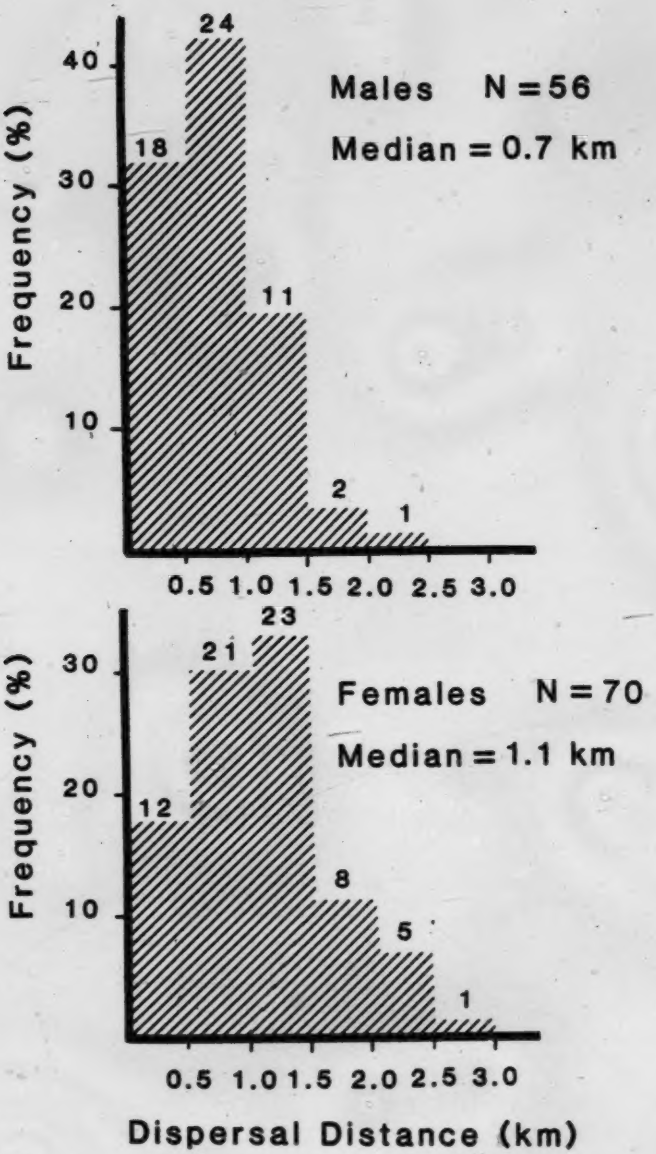

Males N = 24
Median = 0.9 km
Frequency (%)
30
20
10
6
7
5
5
1
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
Females N = 42
Median = 1.4 km
Frequency (%)
30
20
10
6
12
5
7
4
3
1
4
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 +
Dispersal Distance (km)

FIGURE 5.2. Dispersal distances for non-radioed blue grouse, 1979-1983. Sample sizes are indicated above the histogram.


Frequency (%)
40
30
20
10
24
18
11
2
1
Males N = 56
Median = 0.7 km
0.5 1.0 1.5 2.0 2.5 3.0
Frequency (%)
30
20
10
23
21
12
8
5
1
Females N = 70
Median = 1.1 km
0.5 1.0 1.5 2.0 2.5 3.0
Dispersal Distance (km)

6. FACTORS INFLUENCING NATAL DISPERSAL OF BLUE GROUSE

6.1 Introduction

Natal dispersal, the movement of an animal between its place of birth and the place where it first reproduces (Howard 1960, Greenwood and Harvey 1982), may have important implications for gene flow, colonization of new habitats, and limitation of population size (Johnston 1961, Krebs and Myers 1974, Lidicker 1975, Gaines and McClenaghan 1980, Watson and Moss 1979, Swingland and Greenwood 1983, and others). Dispersal prior to breeding is often looked upon as an important cause of population limitation and is frequently associated with a specific time of year when population limitation is thought to occur (Watson and Moss 1979). Much of the previous work on avian dispersal concerns descriptions of patterns and is based on the recovery or reobservation of marked birds. Frequently, the nature of the dispersal process is inferred from data on distances and timing of disappearance of birds from the population but there have been few attempts to investigate the actual dispersal process by following individual birds.

Natal dispersal of birds is potentially influenced by 4 different movements: (1) summer movements away from the nest, (2) fall migration to wintering areas, (3) spring migration to breeding areas, and (4) spring movements after arrival on breeding range. The relative influence of any of these variables on dispersal is not well understood.

Radio-tagging animals makes the study of the dispersal process more feasible than conventional methods which usually involve the marking and infrequent resighting of each individual. By radio-tracking young blue grouse (*Dendragapus obscurus*), I was able to assess the effects of 3 of the above movements (fall migration, spring migration, and spring movements on breeding range) on net dispersal distance. The results and their implication for the limitation of populations are discussed in this paper.

6.2 Study Area and Methods

The study was conducted on Hardwicke Island, British Columbia, Canada (50° 28' N, 125° 50' W) from 1979 to 1982. Much of the coastal coniferous forest on the 77-km² island had been logged or burned in the preceding 100 years, and as a result, a wide variety of successional stages were present. Western hemlock (*Tsuga heterophylla*) was the most abundant tree on the island and a variety of shrubs, ferns, and other herbaceous plants abounded in recently-logged areas (Niederleitner 1982, Hines 1986*a*). Early successional stages (≤20 years in age) were especially preferred by breeding blue grouse and supported population densities several times greater than those occurring in second-growth and mature forests (Niederleitner 1982). Mature forests (>250 years in age) were preferred wintering areas but earlier successional stages were also used extensively by wintering grouse. Mid-successional stages (21-100 years in age) were less frequently used in winter (Hines 1986*a*). The relative abundance of different seral stages in 1979 was: ≤10 years in age, 12%; 11-20 years, 9%; 21-50 years, 40%; 51-100 years, 16%; 101-250 years, 2%; >250 years, 16%; and private land (unclassified to forest type), <5%. Logging operations reduced the amount of mature forest to 14% between 1979 and 1982.

Dispersal of young blue grouse was studied by radio-tracking. In late summer and fall, 1979-81, 235 juvenile blue grouse were equipped with radio packages; 25 females and 14 males lived long enough or could be located frequently enough to provide detailed information on movements from late summer of one year to the following spring. Radio packages were mounted as backpack units (Brander 1968) weighing 2 to 6% of the body weight of juveniles at the time of marking. More than 95% of the 235 radio-marked birds originated from a 465-ha study area (where breeding populations were being studied intensively) and all but 2 grouse were captured within 0.5 km of this site. Radio-marked grouse were located with a portable receiver and 4-element yagi antenna. Locations were determined by moving to within 20 m of the bird or by triangulating from short distances (<100 m).

Four types of movements considered in this study were defined as follows: (1) fall migration - the movement from summer to winter range, (2) spring migration - the movement from winter to summer range, (3) movements on breeding range (abbreviated *MOBR*) - movements once the grouse had arrived at a potential breeding area, and (4) dispersal - the net movement between place of birth and place of breeding. Mean location during summer and mean location on winter range were used in the computation of fall migration distance. Mean location in winter and first location of a grouse when it completed spring migration were used in the calculation of spring migration. Migration movements by blue grouse are relatively quick and unidirectional, typically involving movements of 1 km or more per day (Lance 1970, Sopuck 1979). Grouse were said to have completed spring migration when such movements no longer occurred. If available, the locations of nests for females or the sites where males were seen as territorial adults were used as final locations on breeding range. Such information was not available for 9 males and 5 females, and centers of activity (Hayne 1949) during localization were used as an approximation of location of breeding for these grouse. This was thought to be valid because adult grouse show fidelity to sites where they settle as yearlings (Sopuck 1979, Jamieson and Zwickel 1983*a*).

The effect of each type of movement on dispersal distance was evaluated by both simple and multiple linear regression. In these analyses dispersal distance was the dependent variable and sex, fall migration distance, spring migration distance, and movements on breeding range were independent variables. Sex of the grouse was treated as a "dummy" variable in the regression (Kleinbaum and Kupper 1978:188). Directions of movements were analysed using circular statistics (Batschelet 1981).

To summarize information on movement patterns, fall migrations were described as "long" if they exceeded the median distances of 2.3 km for females and 1.9 km for males, or "short" if they were less than these values (Hines 1986*b*). Long and short spring migrants were identified on the basis of median distances of 1.0 km for females and 1.4 km for males (unpublished data). Criteria for long- and short-distance dispersers were median dispersal distances of 0.9 and 1.4 km for males and females, respectively (Hines 1986*c*).

6.3 Results

6.3.1 General Description of Movement Patterns

Descriptive statistics on seasonal movements of the 39 grouse are summarized in Table 6.1. Fall migrations, spring migrations, and movements on breeding range differed in distance (Kruskal-Wallis test, $P < 0.01$) and pairwise contrasts indicated that movements on breeding range were shorter than either fall or spring migrations ($P < 0.05$). In contrast, fall and spring migrations were similar in length ($P > 0.05$). Thus, fall and spring migrations had greater potential to influence dispersal distance than did *MOBR*.

Migration distances varied greatly among individuals. Thirteen grouse moved relatively long distances in fall (i.e., greater than the median distance); 10 wintered in older habitats ($>$20 years in age) and 3 settled in earlier successional stages ($\leq$ 20 years in age). All 10 that settled in mature habitats migrated long distances in spring whereas 2 of 3 that settled in earlier successional stages remained near where they had wintered. Twenty-six grouse moved relatively short distances in fall, 19 wintered in early successional stages and 7 settled in older seres. Sixteen of the 19 that wintered in early successional stages migrated only short distances in spring and 3 moved long distances. Six of 7 juveniles that moved short distances and wintered in older forest, moved long distances in spring.

Movements on breeding range varied from 0 to 1.4 km for males and 0.1 to 2.6 km for females but could not be predictably associated with previous movements in fall or spring. For example, 7 of 13 grouse that moved long distances in fall made long *MOBR* and 13 of 26 individuals that made short migrations in fall had long *MOBR*. The relationship between spring migration and *MOBR* was similar. Ten of 20 grouse that migrated long distances in spring also moved long distances on breeding range. Ten of 19 short-distance spring migrants had long *MOBR*.

Directions of movements on breeding range, based on consecutive locations, were evaluated for 21 females observed 10 or more times in the prenesting period. In no instance did these movements show directional patterns (Rayleigh's test, $P > 0.10$). Thus, movements on breeding range were not dispersive in the sense of taking a young grouse in a consistent direction away from its place of hatch.

6.3.2 Effects of Various Movements on Dispersal

Twelve of 22 short-dispersers were relatively sedentary and did not move far from their place of birth in any season (Figure 6.1). The other 10 moved away in fall but returned to near their place of birth in spring.

Long-distance dispersers showed less distinct patterns. Six grouse moved away from their natal areas in fall and settled in spring near where they wintered (Figure 6.1). Four other grouse migrated substantial distances in both fall and spring but did not return close to their place of hatch. Dispersal of 7 other grouse seemed to be a product of fall migration, spring migration, and *MOBR* with none of these movements having a clearly dominant influence. Thus, longer-distance dispersals in blue grouse were not consistently associated with one type of movement pattern (Figure 6.1).

Linear regression revealed no obvious simple relationship between dispersal distance and: (1) sex ($r = 0.09$, $P = 0.59$), (2) distance moved during fall migration ($r = 0.21$, $P = 0.19$), (3) distance moved during spring migration ($r = 0.06$, $P = 0.72$), or (4) *MOBR* ($r = 0.07$, $P = 0.65$) for the 39 grouse. Thus, any relationship between movement patterns and dispersal must have been of a more complex nature. Inclusion of all 4 independent variables in a multiple regression analysis revealed a significant relationship among the variables ($R = 0.50$, $P = 0.04$). The equation which best fit the data was:

$$Y = 1.11 + 0.41F - 0.37S$$

where Y was dispersal distance (km), F was fall migration distance, and S was spring migration distance. Both F and S had significant slopes (0.41 ± SE 0.13 and -0.37 ± 0.13, respectively; $P < 0.01$) but the slopes for sex ($b = -0.02 \pm 0.23$, $P = 0.92$) and *MOBR* ($b = -0.17 \pm 0.20$, $P = 0.40$) were not significant and excluded from the equation. My interpretation of this analysis is that long dispersal movements were frequently brought about by long movements in fall followed by short movements in spring.

The lack of a higher correlation between dispersal distance and either fall or spring migration distance when considered separately may have occurred because fall and spring migrations frequently counterbalanced each other. Juveniles that moved longer distances in fall often moved long distances in spring (Figure 6.2) and returned toward the general area in which they hatched (Hines 1986*b*).

In Figure 6.2, grouse that dispersed longer than the median dispersal distance (termed "long-dispersers") are indicated by open triangles (for males) or open squares (for females). Note that the points indicating long-distance dispersers are usually farther from the regression line. Thus, long-distance dispersers were grouse that differed from the norm in that they did not move the same distance in spring as they had in fall.

The previous description of movement patterns suggested that spring migration might be influenced by habitat age as well as how far a grouse moved in fall. This possibility was examined further through multiple regression. Both fall migration distance (F, in km) and age of winter habitat (HA, in years) were included in the equation ($Y = -0.192 + 0.893F + 0.004HA$, $R = 0.95$, $P < 0.01$) and the overall relationship accounted for 91% of the variation in distance of spring migration (Y).

6.4 Discussion

Natal dispersal in blue grouse was not a simple one-step process. Some grouse that dispersed longer distances had moved longer distances in fall and subsequently did not move far in spring. These grouse apparently encountered suitable breeding areas (early successional stages) close to where they wintered. Other grouse became long-dispersers by moving long distances in both fall and spring or as a product of fall migration, spring migration and movements on breeding range. In contrast, some grouse migrated long distances in fall, returned to near their place of birth in spring, and dispersed only short distances. These grouse typically wintered in mid-successional stages (>20 years in age) or mature forests (>250 years in age) that were not suitable breeding habitat. Other short-distance dispersers did not move far in fall and wintered in early successional stages (≤20 years in age) that were suitable for breeding. In spring their movements were fairly restricted.

After a grouse arrived on breeding range, its movements were not predictably associated with dispersal. *MOBR* for any given individual did not follow a directional pattern and hence would not necessarily lead an animal away from its place of birth. Further, *MOBR* were relatively small compared with fall and spring migration and thus, had less potential to influence dispersal. The biggest influence *MOBR* had on dispersal was likely additive. Some individuals became long-dispersers because of the additive effects of fall, spring, and *MOBR* that were all short but in the same general direction.

Multiple regression analysis suggested that there was a general pattern of dispersers moving long distances in fall and short distances in spring. This relationship accounted for about 25% of the variability in dispersal distance indicating that other factors were involved also. The fact that much of the suitable breeding habitat on Hardwicke Island was located on or near the main study area where most radio-marked grouse originated, may have influenced the results. If suitable breeding habitat had been more available elsewhere then the correlation between fall migration and dispersal distance may have been stronger with more grouse encountering breeding areas close to where they wintered (and not returning to near their place of hatch in spring).

If, as the present data suggest, fall and spring migrations influence dispersal, it is essential to understand why migration distances vary so much among individuals. Spring migration distance seemed to be adequately explained by 2 variables: how far a grouse moved in fall and whether it wintered in or near a habitat that was suitable for breeding. The factors influencing fall migration are less clear. One possibility, that some grouse migrate with their mothers and hence move longer distances (Schroeder 1985), seems unlikely as most broods had broken up before migration (Hines 1986*d*). A second alternative, that grouse migrate in fall and settle where they first encounter a suitable winter habitat (Schroeder 1985), also seems unlikely. Although the distribution of suitable habitat undoubtedly influences where grouse can settle, many migrant grouse pass through suitable wintering areas without stopping. A third alternative, which is difficult to evaluate at present, is that the propensity to move is innate (Greenwood et al. 1979). Data on blue grouse suggest that siblings disperse similar distances (Jamieson and Zwickel 1983*a*) and this somewhat supports the contention that dispersal distance has an innate, heritable component.

Based on the previous data and discussion, I propose the following model of the dispersal process in blue grouse. Grouse move variable distances to winter range in their first fall, the distance depending on the bird's innate tendency to move and where it encounters suitable winter habitat. The distance a grouse moves in spring depends on where it first encounters suitable breeding habitat. Grouse that find breeding areas close to where they winter do not move far in spring; others do not encounter suitable breeding areas until they return to their natal areas. Once on breeding range, young grouse wander in search of vacant habitat and interact with resident birds as suggested by Sopuck (1979), Hannon et al. (1982), and Jamieson and Zwickel (1983*b*). Such *MOBR* are not dispersive in the sense of always being oriented away from the place of birth but sometimes they add on to total dispersal distance and may be one of the reasons grouse disperse longer distances.

Dispersal is hypothesized to play an important role in limitation of populations (Watson and Moss 1979, Moss et al. 1982, and others). What then are the implications of the present data on dispersal with regard to limitation of populations of blue grouse? Hypotheses about the role of dispersal in population limitation are essentially behavioral ones and, to demonstrate that dispersal limits population size, one needs to show the existence of a behavioral mechanism that influences dispersal patterns. In blue grouse, movements on breeding range are probably influenced by social interactions (Sopuck 1979, Hannon et al. 1982) but the data for Hardwicke Island suggest that *MOBR* have less influence on dispersal than either fall or spring migrations. If dispersal is involved in limitation of blue grouse populations then one needs to explain especially what determines fall migration distance (spring migration is adequately explained by how far a grouse moves in fall and age of the habitat that the grouse uses in winter). Fall movements occur at a time of year when blue grouse are not territorial and show little overt aggression. Thus, if socially-induced dispersal is involved in limitation of blue grouse numbers, the influence of behavioral interactions must be of a more subtle nature. Whether such interactions occur or whether they can influence dispersal remains an open question.

6.5 Summary

Dispersal of blue grouse was studied by radio-tracking 14 juvenile males and 25 juvenile females from late summer until they settled on breeding range in the following year(s). Fall and spring migrations or movements on breeding range showed no simple correlation with dispersal distance. Inclusion of all variables in a multiple regression equation suggested that grouse dispersing longer distances tended to migrate relatively long distances in fall and short distances in spring. However, this relationship accounted for only 25% of the variation in dispersal distance. Further analyses indicated that grouse that dispersed less than the median distance (0.9 km for males, 1.4 km for females) usually made short migrations in fall, wintered in early successional stages that were suitable as breeding habitat ($\leq$20 years in age), and subsequently did not move far in spring. Other short-distance dispersers moved longer distances in fall, settled in older habitats that were not useful for breeding, and returned to near their place of birth in spring. Long-distance dispersal occurred when grouse migrated long distances in fall and settled in early successional stages near where they wintered, when grouse moved long distances in both fall and spring but did not return to near their place of birth, or through a combination of movements at all times of year. Therefore, dispersal was a complex process not easily attributed to a particular time of year or a particular type of movement pattern. The implications of these findings for limitation of populations are discussed.

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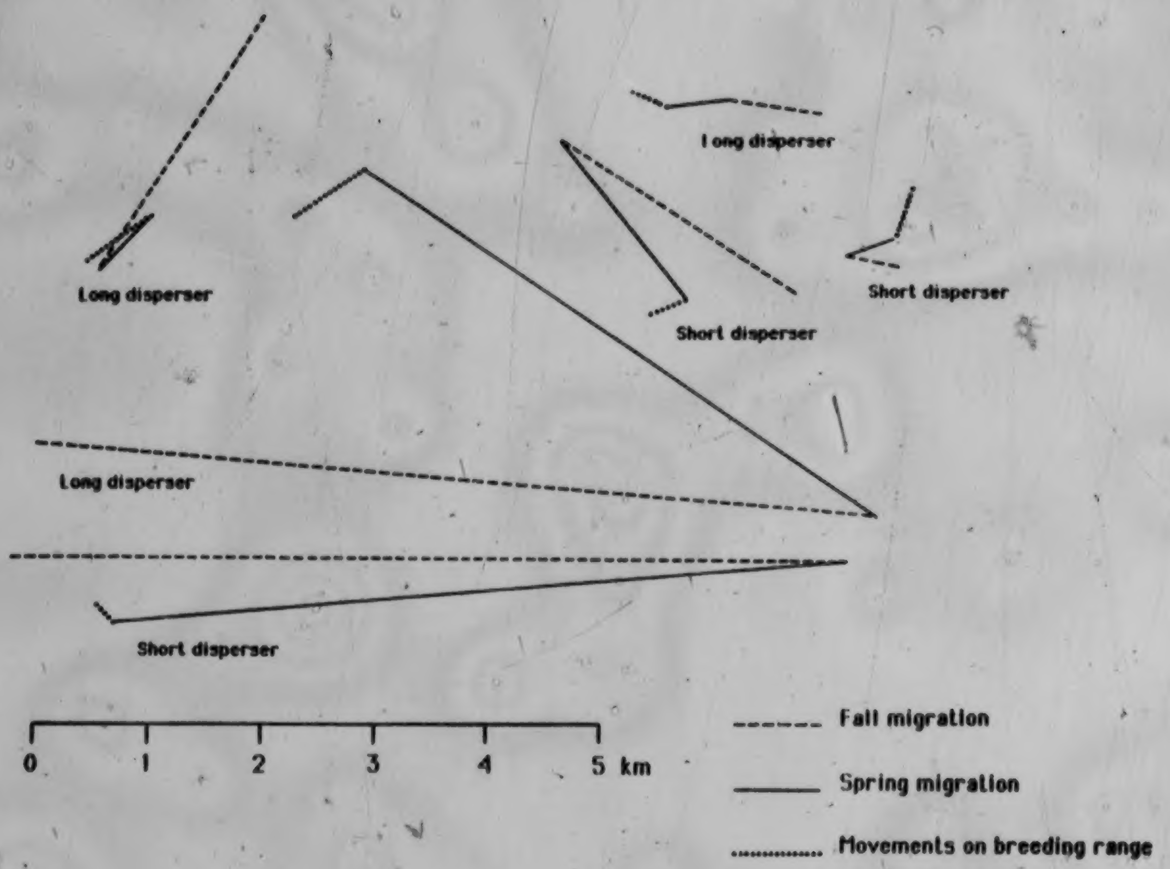
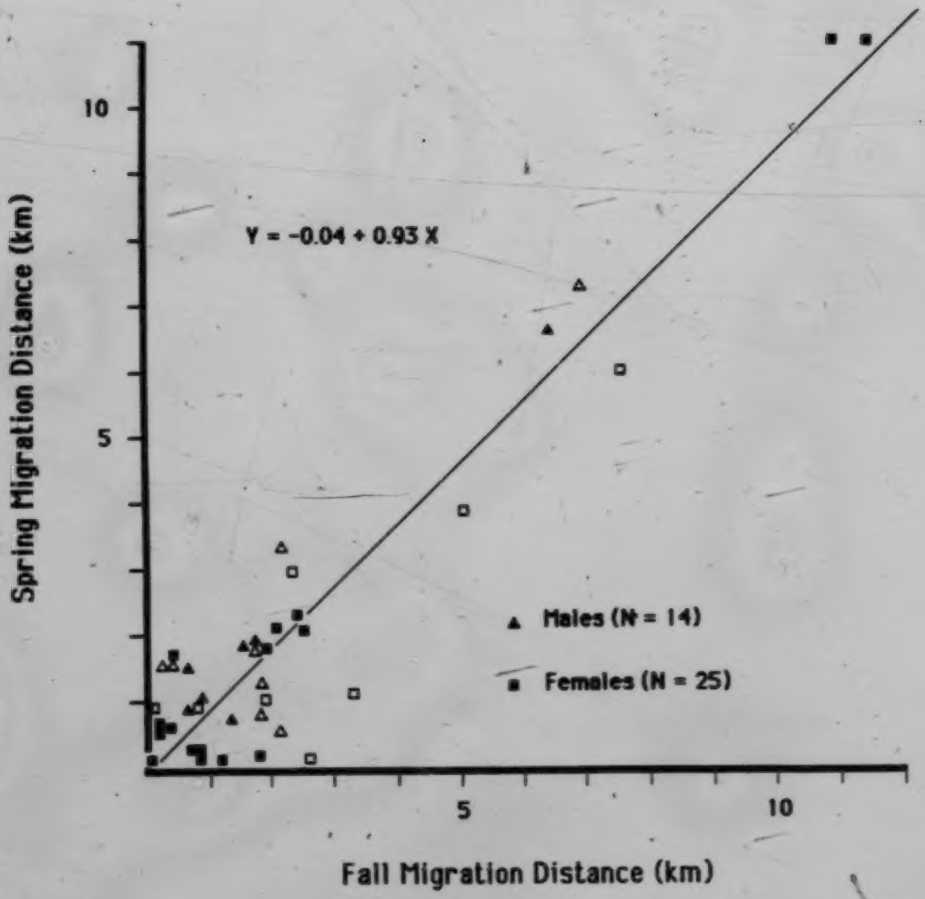

Long disperser
Long disperser
Short disperser
Short disperser
Short disperser
Long disperser
0
1
2
3
4
5 km
Fall migration
Spring migration
Movements on breeding range

FIGURE 6.2. Regression of spring migration distance (km) on fall migration distance (km) and the effect of this relationship on dispersal. Triangles indicate males, squares indicate females, open symbols are "long" dispersers, and darkened symbols are "short" dispersers.


Spring Migration Distance (km)
10
5
Y = -0.04 + 0.93 X
▲ Males (N = 14)
■ Females (N = 25)
5
10
Fall Migration Distance (km)

7. RECRUITMENT IN A DECLINING POPULATION OF BLUE GROUSE

7.1 Introduction

Recruitment, the process whereby new animals are added to a population, is instrumental in determining the size of breeding populations of many species of birds and mammals (Tanner 1966, Bendell 1972). Several reviews of avian population ecology suggest there is a fall to spring bottleneck which eliminates many young animals from the breeding population either through death, dispersal, or failure to breed (Wynne-Edwards 1962, Lack 1966, Bendell 1972) and 2 major hypotheses have been proposed to explain this limitation of bird populations. Wynne-Edwards (1962) believed there were more than enough potential recruits surviving through winter than were needed to replace dying adults. He hypothesized that social behavior prevented some individuals from breeding, thereby checking population growth. In contrast, Lack (1966) thought over-winter mortality of young (which was not socially induced) usually limited numbers of birds.

Similar factors are thought to affect recruitment in populations of grouse. Some authorities view over-winter mortality as critical (Gullion and Marshall 1968, Gullion 1970, Rusch and Keith 1971) whereas others consider social behavior more important (Watson and Moss 1972, Zwickel et al. 1983, Hannon 1983). Many proponents of the spacing behavior hypothesis believe that dispersal plays an important role in population limitation. For example, Watson and Moss (1979) hypothesized that cyclic changes in numbers of grouse were caused by changes in spacing behavior which resulted in cyclic losses of potential recruits due to dispersal or over-winter mortality. Keppie (1979) showed that emigration in spring (the time of year when intraspecific aggression was highest) caused numerical changes in a local population of spruce grouse (*Dendragapus canadensis*).

Blue grouse (*Dendragapus obscurus*) apparently conform to the idea that recruitment determines population size (Zwickel and Bendell 1972, Zwickel et al. 1983). Adult mortality is relatively constant from year to year and populations increase when the number of recruits is high and decrease when the number of recruits is low. Removal experiments, in which resident grouse were eliminated, suggested there were more potential recruits alive in spring than were needed to replace losses of adults (Bendell et al. 1972; Zwickel 1972, 1980). Sopuck (1979) and Hannon et al. (1982) studied spring movements of adult and yearling females on breeding range and found that adults quickly localized on a small home range while yearlings wandered in search for suitable areas to settle. They suggested that adults prevented many yearlings from localizing immediately. Despite this, most (about 90%) of the yearling females eventually nested and therefore were not prevented from breeding. Similarly, Sopuck (1979) and Jamieson and Zwickel (1983) studied recruitment of yearling males and found that most localized (a possible indication of recruitment). These results somewhat contradict those of the removal studies and the question of whether many young animals are prevented from breeding by social behavior remained unanswered.

There were, however, 2 potential biases in the studies of radio-marked blue grouse (Sopuck 1979). One possible problem was that the grouse marked with radios in spring were not representative of the available recruits (i.e. the sample was biased towards recruiting individuals which were easier to capture and radio-mark). Another possibility was that because of low production of young in the summers preceding the radio-tracking studies, the number of yearlings alive in spring was abnormally small, allowing most potential recruits to enter the breeding population (Sopuck 1979).[3]

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[3] This seems unlikely because, according to the definition of Sopuck (1979), "low" production occurred in 5 of 9 years the population was studied (see data in Zwickel et al. 1983). Hence, "low" production was not unusual in this population.

A problem common to most population studies is that young animals, which make up the recruiting portion of the population, are difficult to study. Their disappearance might result from either death or dispersal, or they may live as "floaters" (Brown 1969) or "underworld" animals (Smith 1978) which are not readily observed. Traditional methods of marking and reobserving such animals are not entirely effective in the study of recruitment and a useful additional approach for such investigations is to radio-track a sample of potential recruits. Accordingly, in late summer and early fall 1979 through 1982, juvenile blue grouse were equipped with radio-transmitters on Hardwicke Island, British Columbia. My goal was to identify surplus and recruiting individuals and document losses of young (potential recruits) from the population. Two hypotheses were tested:

Hypothesis 1: the number of recruits is determined by spacing behavior in spring;

Hypothesis 2: the number of recruits is determined by over-winter mortality.

If over-winter mortality limited numbers, I expected to find that most surviving females would breed in spring. If behavior limited density, I expected to find "surplus" animals that were forced to disperse or defer breeding by social pressures (Watson and Moss 1970). Female grouse were particularly emphasized because the number of females that breed is most important in determining population growth in promiscuous or polygynous species such as blue grouse (Brown 1969). Also, it is difficult to directly measure reproductive success of males at present as copulations are rarely seen.

7.2 Study Area and Methods

Hardwicke Island (50° 50' N, 125° 50' W) lies between Vancouver Island and the mainland of British Columbia, Canada. Its surface area is 77 km^2; 465 ha of this make up the main study area for blue grouse research. Plant communities are typical of the western hemlock (*Tsuga heterophylla*) biogeoclimatic zone

(Krajina 1965). Much of the island has been logged and supports a variety of successional stages ranging from newly-logged to greater than 250 years old. The main study area consists largely of seral stages less than 15 years in age. Niederleitner (1982) has detailed the vegetation of such areas.

Methods used in the study of blue grouse populations have been described by Zwickel and Bendell (1967*a*) and Zwickel (1982). Adults, yearlings, and large juveniles were located with pointing dogs, captured with noosing poles (Zwickel and Bendell 1967*b*), and color-banded for future identification. Usually about 80% of the adult males on the study area were color-banded and territories of these, plus unidentified territorial males, were plotted on maps to determine total numbers. Yearling males were secretive and very difficult to census. Therefore, the number of all such grouse identified on the study area was used as an index to the abundance of this cohort. A minimum estimate of the female population was the number of different adult and yearling females identified on the study area each year. Production of young (the number of juveniles present on the study area in late summer) was estimated by multiplying the number of females seen with broods (throughout the summer) by the average brood size in August.

This study involved following a relatively large number of radio-marked grouse throughout the year to determine movements, mortality, and reproductive success. Fall and winter field work was conducted from September through March of 1979-1980 and 1981-1982 but only from September through December in 1980-1981. Limited winter research was undertaken in 1982-1983. Summer field work lasted from April through August in all years. During late summer and fall, juvenile blue grouse were equipped with radio transmitters, mounted as back-pack units similar to those described by Brander (1968). Radio packages weighed from 2 to 6% of the body weight of juveniles at this time and had little obvious effect on survival, reproduction, or movements of grouse (Hines and Zwickel 1985). Numbers of radio-marked grouse were 60 in 1979, 97 in 1980, 78 in 1981, and 58 in 1982, for a total of 293. Solar-powered transmitters used in 1979 and 1980 functioned poorly during winter when weather was cloudy and when grouse tended to inhabit dense coniferous cover with low light levels. Consequently, in the falls of 1981 and 1982, mercury or lithium battery transmitters were placed on birds.

In many instances, fates of radio-marked grouse could not be determined as "alive" or "dead". Instead, fates were classified as follows: (1) surviving over winter (alive on 1 April of the year after hatch); (2) predator kill; (3) miscellaneous deaths (remains of the grouse were found but the cause of death was unclear); (4) believed dead in fall (the bird was lethargic when approached and appeared to be in poor condition; the grouse was not known to migrate, radio contact with it was lost in fall, and it was not seen again); (5) believed dead in winter (the grouse had settled on winter range but radio contact was lost during the winter and the bird was not seen again); (6) migrated and disappeared (the grouse left the study area but was not known to localize on winter range); (7) unknown (the grouse was not known to migrate and the last sighting of it was on summer range; in several instances such grouse were never resighted after being equipped with transmitters); (8) lost transmitter (the radio harness came off the grouse); and (9) killed by radio harness. Animals classified as fate (8) or (9) were eliminated from calculations of over-winter survival.

As indicated above, not all radio-marked grouse provided complete records and in particular, I had difficulty in locating solar-powered radios in winter. Under such conditions, dead animals were less apt to be found. Elimination of all radio-marked grouse with incomplete records from further consideration might severely bias estimates of survival (White 1983); therefore survival over winter was computed in 2 different manners. Ideally one would estimate survival by dividing the number of radio-marked yearlings that lived until spring (1 April) by the number that were marked the previous fall. A basic assumption underlying this estimate is that disappearing grouse are dead and do not have failed transmitters or have not moved beyond the range of the radio signals. If a large number of the grouse of unknown fate were actually alive, survival would be significantly underestimated. I believe that few of these grouse actually survived for several reasons. First, none of the grouse marked with battery-powered transmitters in 1981 migrated beyond signal range, hence I believe this was likely true also for birds marked with solar-powered transmitters in other years. Forty-two of the missing grouse disappeared in winter, a time of year when grouse were sedentary (Hines 1986*a*) and it seemed unlikely that the missing grouse moved out of radio range at this time. Subsequent searches of the mainland supported this viewpoint as none of the missing grouse were found there. Further, I checked (with a pointing dog) the home ranges of many of the grouse that disappeared on winter range but did not find any of the animals. This indicated transmitter failure was an unlikely cause of so many disappearances. Median dispersal distances were 0.9 km for males and 1.4 km for females (Hines 1986*b*) and about half the known survivors returned to the main study area as yearlings. If radio failure had been the major cause of disappearances in fall and winter then one would expect to find numerous grouse with malfunctioning transmitters returning to the main study area in spring. Only one such instance was recorded in 4 years of study, therefore radio failure can be dismissed as the cause of so many losses.

If grouse did not move beyond signal range and failure of radios was not a major cause of disappearances, how can the disappearance of radio-marked grouse be explained? Remains of 4 dead grouse with non-functioning solar-powered transmitters were found during the course of field work. As the probability of finding such grouse was exceedingly low, deaths and associated radio failures were likely quite common and the major cause of missing grouse.

A second, more conservative estimate of survival (Method 2) was computed by eliminating all grouse of unknown fate from the calculations. In this estimate, all grouse that disappeared before localizing on winter range, and those with which radio contact was never made, were considered of unknown fate but birds that disappeared after localizing on winter range were treated as dying.

To determine if survival varied seasonally, I calculated monthly survival rates using a formula similar to that of Trent and Rongstad (1974). Grouse of unknown fate or unknown time of death were excluded from this analysis.

The number of female recruits required to maintain a stable population was the number of adult and yearling females alive one year that had disappeared from the study area by the following year. The number of known recruits (from census data) and the predicted number of recruits (number of juvenile females alive in late summer multiplied by the rate of survival over winter) were compared to this figure. This indicated whether survival of juveniles over winter was adequate to maintain a stable population.

7.3 Results

7.3.1 Survival Over Winter

Fates of radio-marked juveniles are summarized in Table 7.1. A potential bias in these data arises because there were a large number of grouse of unknown fate. If many such grouse actually lived then estimates of survival would be low. Reasons that I believe that most grouse of unknown fate died, were discussed previously.

Mortality of juveniles was most severe in early fall (Figure 7.1). Over 50% of the radio-marked males died by the end of October but after that, survival improved. In autumn, females survived at a somewhat better rate than did males but the rate of decrease for females was slightly steeper in winter.

Monthly survival rates for fall and winter are summarized in Table 7.2. Similar data were not available for late winter in 1980-1981 and survival rates for January through March are based on the 1979-1980 and 1981-1982 samples only. X^2 tests (in the form of 2 x 7 contingency tables) indicated that survival rates of males varied among months ($P < 0.01$). This was possibly true of females also but the relationship was of borderline significance ($P = 0.09$). As indicated by a linear regression of monthly survival rate on dates, survival of juvenile males improved throughout fall and winter ($r = 0.87$, $P = 0.01$). Data for radio-marked females showed a similar trend but were not significant ($r = 0.63$, $P = 0.13$).

Predation by raptors was high during all years and accounted for at least 43% of the known deaths (Table 7.3). Many of the deaths included under "probable predator kills" likely were caused by raptors. Goshawks (*Accipiter gentilis*) were the only raptors seen preying on grouse but red-tailed hawks (*Buteo jamaicensis*) and bald eagles (*Haliaeetus leucocephalus*) inhabited the island during winter and may have taken grouse. The timing of losses of juveniles from the population corresponded to seasonal changes in the abundance of raptors on Hardwicke Island. An index of raptor abundance was greatest in September and October (2.7 hawks observed per 100 hours of field work) and lower from November through March (0.9 hawks per 100 hours). In contrast to raptors, mammalian predators were not numerous and accounted for few mortalities (Table

7.3).

Over-winter survival of juveniles was low each year. Minimum survival (Method 1) of males averaged 21% over 4 years of study (Table 7.4) and that of females was only slightly higher (28%). Survival, estimated by Method 2 (Table 7.5), averaged 28% for males and 35% for females. I used a multidimensional contingency table to determine if survival rates varied between sexes or among years. Survival, estimated by Method 1, did not vary between sexes ($P = 0.20$) or among years ($P = 0.16$). A similar analysis, based on Method 2, gave similar results (for sexes $P = 0.32$, for years $P = 0.74$).

7.3.2 Survival and Reproduction by Yearling Females in Spring

Only 46 females survived over winter during the 4 years of study. Five of these had malfunctioning transmitters and could not be adequately radio-tracked and another lost its radio package, thereby reducing the effective sample to 40 females. Twenty-three (58%) yearlings eventually nested, 12 (30%) died before the end of the breeding period (1 June), and 5 (13%) localized on a small home range but did not nest. The number of females that nested was 2 of 8 in 1980, 3 of 8 in 1981, 12 of 16 in 1982, and 6 of 8 in 1983. The proportion of yearlings that nested varied among years (contingency table, $P = 0.05$).

Twenty-three of 28 radio-marked females, which survived throughout the breeding period, eventually nested. Although sample sizes were very small, it appeared that most females nested in years of lower population density (12 of 12 in 1982 and 6 of 7 in 1983) whereas a smaller proportion nested in the years of higher density (2 of 4 in 1980, 3 of 5 in 1981). These differences were of borderline significance (contingency table, $P = 0.07$).

Another index of recruitment is the proportion of yearlings sighted on the study area in a given year that are known to have nested. Known breeders included females that were found on a nest, seen with a brood, or having a brood patch (an indicator of incubation). All other females were designated as probable non-breeders. The estimated proportion of females that nested was 59% in 1980 ($N = 87$), 67% in 1981 ($N = 52$), 81% in 1982 ($N = 42$), and 82% in 1983 ($N = 27$). A X^2 contingency table revealed that these proportions differed significantly ($P = 0.03$); in the later years of study, relatively more of the yearling females bred.

7.3.3 Population Trends and Recruitment

Numbers of all sex and age classes declined steadily from 1979 to 1983 (Figure 7.2). Recruitment, as indicated by the number of yearling males and yearling females observed on the study area, decreased steadily also. To find out if production of young had any influence on the number of recruits in the following year, I used a linear regression analysis (Figure 7.3). Number of female recruits proved to be significantly correlated with production of young in the previous year ($P = 0.03$) but the relationship for males was of borderline significance ($P = 0.08$).

The number of recruits needed to maintain a stable population of females is shown in Table 7.6. With the possible exception of 1979-1980, production of young and subsequent survival over winter was not adequate to maintain population stability in any of the years of study.

7.4 Discussion

The breeding population of blue grouse on Hardwicke Island declined steadily from 1979 to 1983 and production of young followed a similar course. Increasing and stable populations of blue grouse on Vancouver Island were studied during similar stages of plant succession, with similar techniques, indicating that the population decline likely was not induced by either plant succession or research methodology. A major difference between studies in the 2 areas was that juveniles were not equipped with transmitters on Vancouver Island whereas a large sample of juveniles was radio-marked on Hardwicke. If radio-marked grouse survived or reproduced more poorly than other grouse, the results of this study might be greatly biased. This was not the case (Hines and Zwickel 1985) and I conclude that low rates of recruitment were not caused by radio-marking large samples of juveniles.

In all 4 years of study, mortality of young grouse was high during fall and winter, with predators (especially raptors) the most important cause of losses. Mortality of males was severe in September and October but somewhat lower during winter. Although the statistical relationships were not clear, females also may have suffered highest mortality in early fall. Over the period of study, 84% of the fall and winter mortality of males and 66% of the mortality of females occurred by 1 December. By spring, only 1/4 of the juvenile males and 1/3 of the juvenile females were still alive and, on average, the number of potential recruits alive in spring averaged only 51 to 80% of that needed to replace adults and yearlings that died in the preceding year. Despite the apparent shortage of recruits in all years, not all yearling females nested, and the proportion that nested varied inversely with population density. This suggests that behavior may have prevented some yearlings from breeding in years of high density but does not indicate that spacing behavior caused the decline.

Two major hypotheses, frequently considered as simple alternatives in the regulation of avian populations, were presented at the outset of this paper. I suggested that if social behavior limited recruitment (and hence population size), a surplus of non-breeding yearlings should be present in spring. If over-winter mortality determined numbers, then most young grouse that survived the winter should breed. The social behavior hypothesis is contradicted by the apparent shortage of potential recruits that survived until spring. In contrast, there were non-breeders present in years of high population density suggesting that some yearling females were prevented from breeding under such conditions. The over-winter mortality hypothesis predicts that most females that survive the winter will breed. This was certainly true in the latter 2 years of study when population densities were low (18 of 19 radio-marked yearlings that survived throughout spring nested in 1982 and 1983 and a greater proportion of non-radioed females appeared to breed) but did not appear to be true in 1980 and 1981 (when only 5 of 9 females nested and proportionately fewer of the other females showed signs of breeding). Thus, the data do not clearly support or contradict either hypothesis of population limitation although the evidence that high over-winter mortality caused the population to decrease is strong.

The view that over-winter mortality and social behavior are the only 2 alternatives in the limitation of recruitment to avian populations is overly simplistic because a third factor, production of young in one year, also seemed to influence the number of recruits in the following spring. As survival of juveniles over winter was relatively constant from year to year, variation in the number of potential recruits available in spring was mainly influenced by variations in production. I conclude that if populations are well below some upper limit set by social behavior, the number of young produced one year can become an important factor in determining the size of the subsequent breeding population.

Predation (especially by raptors) was the main cause of losses from the population of blue grouse on Hardwicke Island. Predators accounted for a minimum of 45% of all known mortality and possibly for as much as 71% of all deaths. Other studies of galliforms also show that predation is an important proximate cause of death (Jenkins et al. 1964, Gullion and Marshall 1968, Rusch and Keith 1971, Dumke and Pils 1973). One view, especially attributed to Errington (1946, 1956), is that predators take only a "doomed" surplus and that social behavior is important in bringing this about. Other authorities think of predators as taking many healthy animals and not preying just on a specific, definable surplus (Rusch and Keith 1971). Mortality of young blue grouse was high during fall and winter, a time when I saw no evidence of overt aggression among grouse. Therefore, it was improbable that social behavior at this time of year caused certain juveniles to be more susceptible to predation than others. Grouse captured in winter and those arriving on breeding range in spring are heavy and apparently in good physical condition. Hence, I believe that the susceptibility of young blue grouse to predators was not influenced by food quantity or quality. The density of breeding grouse on the main study area in 1979 and 1980 averaged about 60 females per km^2 -- one of highest densities of grouse (of any species) reported in the literature. Perhaps functional or numerical responses of predators to the high density of blue grouse on Hardwicke Island, coupled with years of low production of young, were important in reducing recruitment and causing the population to decline.

On both Hardwicke and Vancouver Islands numbers of breeding blue grouse were greatly influenced by recruitment in spring but the data for Hardwicke Island differ in several ways from those obtained from increasing, stable, or slowly declining populations on Vancouver Island (Zwickel and Bendell 1972, Zwickel et al. 1983). Removal experiments on Vancouver Island suggested there were many non-breeding yearlings present in spring (Bendell et al. 1972, Zwickel 1972, 1980). In contrast, experimental removals of territorial males on Hardwicke Island conducted by Lewis (1984) indicated that the number of non-territorial yearling males was much smaller on Hardwicke Island than Vancouver Island. Annual production of young on Vancouver Island was thought to be high enough in all years to maintain stable populations but this did not appear to be the case on Hardwicke Island where production and subsequent rates of recruitment were highly correlated. The factors that influence production of young are not well understood and deserve further study.

Finally, one should note that the causes of a population decline, or the factors involved in limiting a population that is at a low density (relative to the carrying capacity of the area), need not be the same as the causes of population limitation at relatively higher densities. The present data suggest that spacing behavior may be important in limiting population density when numbers are relatively high but of less significance at lower densities. At relatively lower densities, over-winter mortality and production of young are apt to be important in limiting population growth. As low density situations may be as typical of animal populations as the high density populations usually studied by ecologists, the need for studies under the former conditions cannot be over-emphasized.

7.5 Summary

Recruitment, the process whereby new animals are added to a population, is thought to be important in limiting growth of avian populations. In populations of blue grouse far more young are produced annually than are needed to replace dying adults. Hypothetically, numbers of recruits might be determined by: (a) how well young survive over winter, or (b) spacing behavior in spring which prevents some young birds from breeding. From 1979 to 1983, these hypotheses were tested on a declining population of blue grouse by radio-marking young in late summer and fall (*N* = 293) and following them until they died or recruited. Survival of young grouse over winter was fairly constant among years averaging 21-28% for males and 28-35% for females. Predators (mainly raptors) caused 45-71% of the losses. For a 465-ha study area, the number of young surviving until spring averaged only 51-80% of that needed to maintain a stable population; this result supported the view that high mortality over winter caused the population to decline. Most yearling females nested when population densities were lower but proportionally fewer yearlings nested when densities were high indicating that the influence of spacing behavior was stronger under conditions of higher population density. A third factor, production of young (number of young alive in August), was correlated with the number of recruits in the following spring and likely influenced recruitment. The latter result was not consistent with either the over-winter mortality or spacing behavior hypotheses. In this population, the number of recruits appeared to be influenced by the number of young produced in a given year, their subsequent survival over winter, and behavioral interactions in spring. The relative importance of each of these variables may depend on population density.

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TABLE 7.1. Fates of 293 radio-marked juvenile blue grouse on Hardwicke Island, British Columbia.

Fate	Number	Percent
Surviving over winter	70	24
Found dead	104	35
Believed dead (fall)	8	3
Believed dead (winter)	42	14
Lost transmitter[a]	14	5
Migrated and disappeared	10	3
Unknown	45	15
Total	293	99

[a] Radio package came off grouse or transmitter removed.

TABLE 7.2. Monthly variations in survival of radio-marked juvenile blue grouse on Hardwicke Island, British Columbia, 1979-1982. Data for September through December are from 1979-1981; data for January through March are for 1980 and 1982 only.

	Percent survival (*N*)	
Month	Males	Females
September	64 (80)	75 (114)
October	71 (51)	87 (86)
November	81 (36)	84 (75)
December	93 (29)	91 (63)
January	94 (17)	81 (43)
February	88 (16)	86 (35)
March	93 (14)	93 (30)

TABLE 7.3. Causes of fall and winter mortality of 104 radio-marked juvenile blue grouse on Hardwicke Island, British Columbia.

Cause	Number	Percent
Killed by raptor	44	42
Probable predator kill[a]	27	26
Killed by hunter	23	22
Caused by harness	4	4
Killed by mammal	3	3
Other	3	3
Total	104	100

[a] Apparent predator kill but also signs of being eaten by scavenger.

TABLE 7.4. Over-winter survival of radio-marked juvenile blue grouse on Hardwicke Island, British Columbia, 1979-1983 (estimated by "Method 1").[a]

	Percent survival (N)	
Year	Males	Females
1979 - 1980	23 (26)	26 (31)
1980 - 1981	17 (41)	21 (47)
1981 - 1982	24 (25)	42 (48)
1982 - 1983	22 (23)	24 (34)
All years	21 (115))	28 (160)

[a] See text for methodology.

TABLE 7.5. Over-winter survival of radio-marked juvenile blue grouse on Hardwicke Island, British Columbia, 1979-1983 (estimated by "Method 2")[a].

	Percent survival (N)	
Year	Males	Females
1979 - 1980	26 (23)	30 (27)
1980 - 1981	28 (25)	29 (34)
1981 - 1982	25 (24)	43 (46)
1982 - 1983	33 (15)	31 (26)
All years	28 (87)	35 (133)

[a] See text for methodology.

TABLE 7.6. Annual losses of female blue grouse on the main study area, Hardwicke Island, British Columbia, 1979-1983, compared with the number of recruits available to replace these losses.

Year	Number of females alive in spring	Number surviving until following year	Number dying	Number of recruits (Estimate 1)[a]	Number of recruits (Estimate 2)[b]	(Estimate 1 - number dying)	(Estimate 2 - number dying)
1979-1980	301	189	112	125 (1.12)[c]	87 (0.78)[c]	+13	-25
1980-1981	276	156	120	90 (0.75)	52 (0.43)	-30	-68
1981-1982	208	120	88	77 (0.88)	42 (0.48)	-11	-46
1982-1983	162	86	76	34 (0.45)	27 (0.36)	-42	-49

[a] Estimated by multiplying production by survival over winter (survival estimated by method 2).

[b] Actual number of yearling females sighted on study area.

[c] Number of recruits as a proportion of the number needed to maintain a stable population is indicated in parentheses.

FIGURE 7.1. Timing of fall and winter losses of radio-marked juvenile blue grouse on Hardwicke Island, British Columbia, 1979-1982.

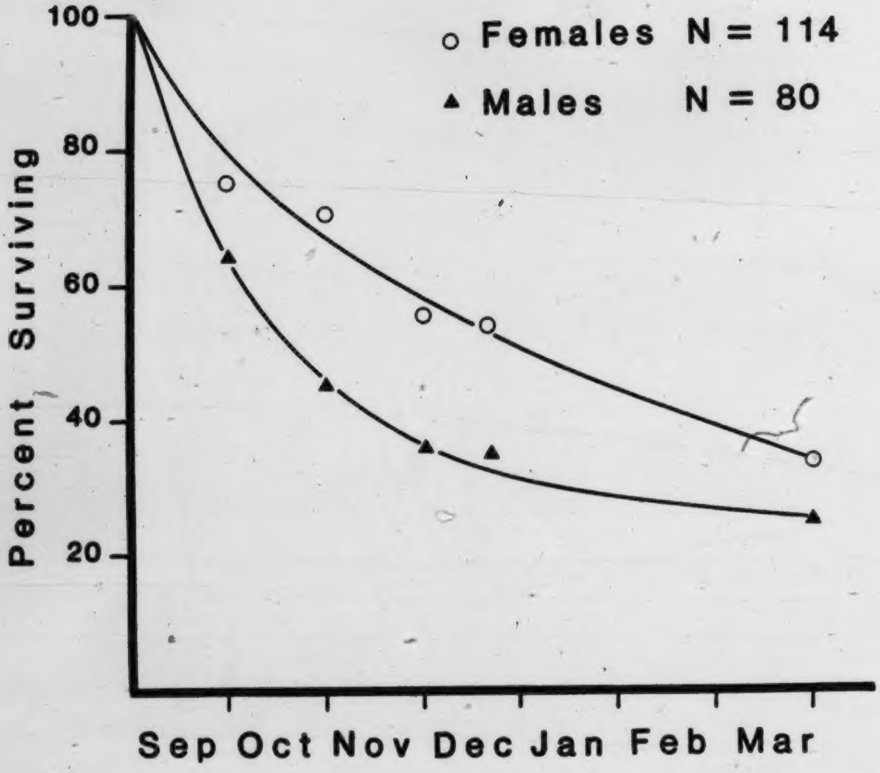

○ Females N = 114
▲ Males N = 80
Percent Surviving
100
80
60
40
20
Sep
Oct
Nov
Dec
Jan
Feb
Mar

FIGURE 7.2. Numbers of blue grouse found on the main study area, Hardwicke Island, British Columbia, 1979-1983.

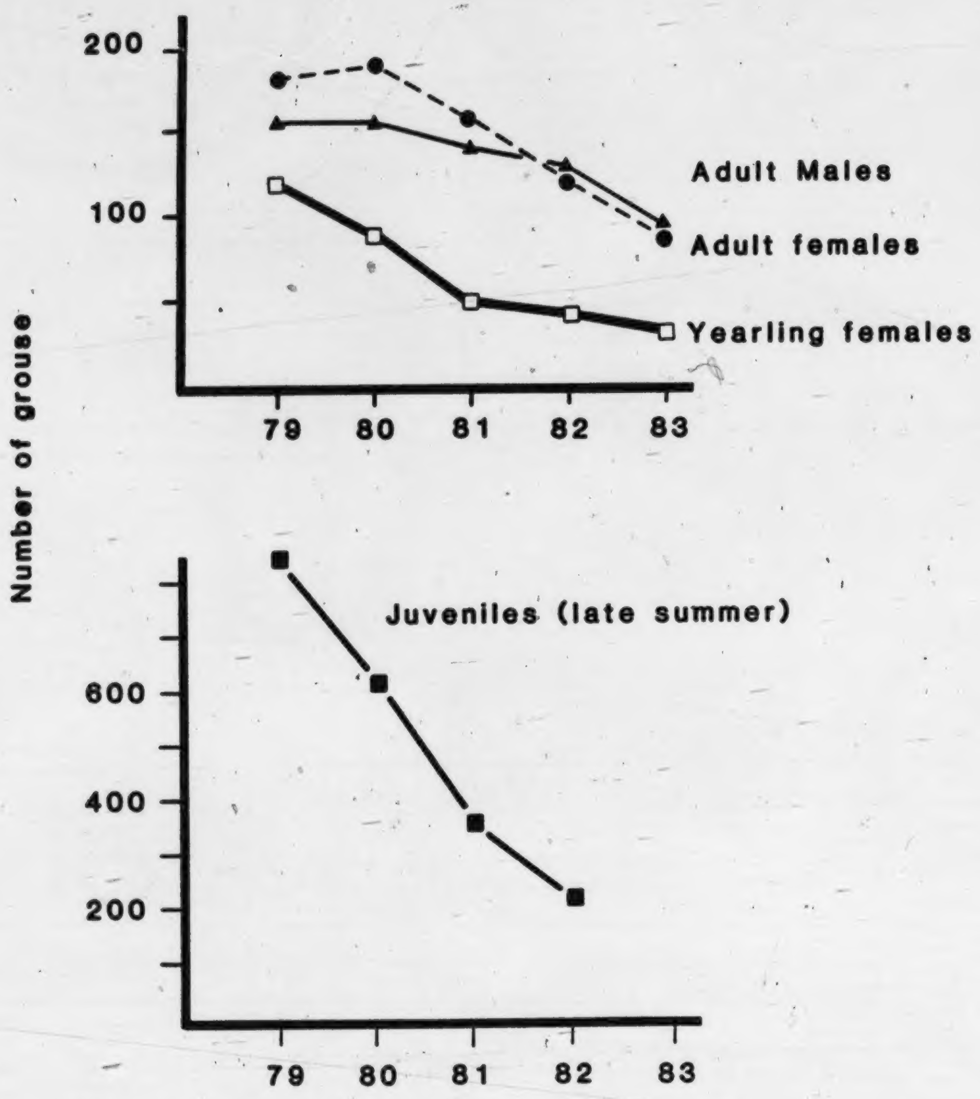
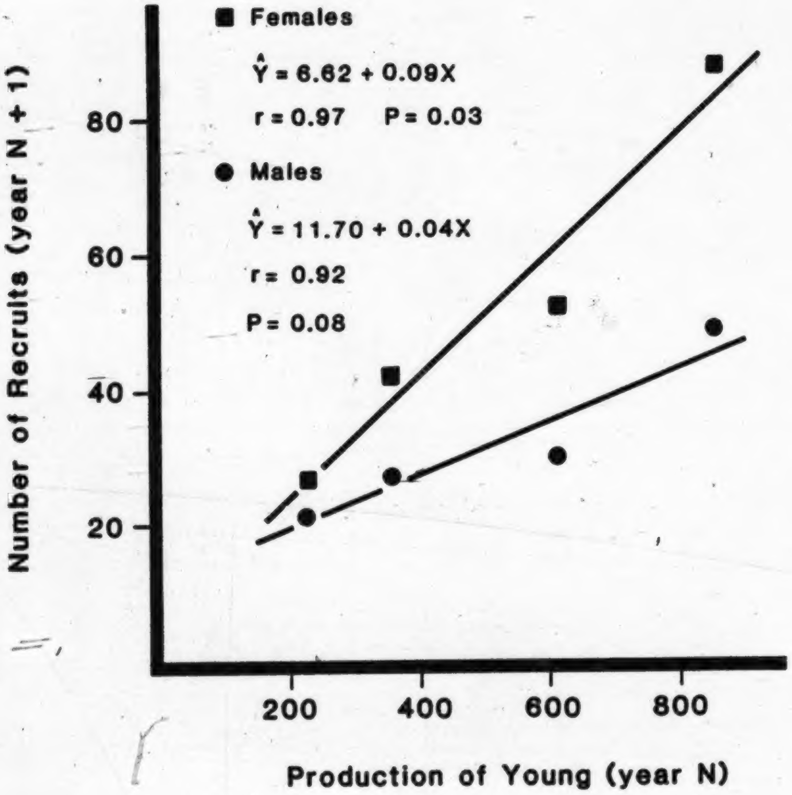

200
100
Adult Males
Adult females
Yearling females
79
80
81
82
83
Number of grouse
Juveniles (late summer)
600
400
200
79
80
81
82
83

FIGURE 7.3. The relationship between the number of recruiting blue grouse and the number of young produced on the main study area in the previous year.


■ Females
$\hat{Y} = 6.62 + 0.09X$
r = 0.97 P = 0.03
● Males
$\hat{Y} = 11.70 + 0.04X$
r = 0.92
P = 0.08
Number of Recruits (year N + 1)
20
40
60
80
200
400
600
800
Production of Young (year N)

8. SPACE: THE FINAL FRONTIER? -OR- MOVEMENTS AND SPATIAL RELATIONSHIPS OF FEMALE BLUE GROUSE IN SPRING

8.1 Introduction

Territorial or spacing behavior has been implicated in the limitation of populations of many avian species (Wynne-Edwards 1962, Brown 1969, Klomp 1972, Patterson 1980) with most such work emphasizing monogamous birds and particularly the effect of male behavior on breeding densities. There is, however, increasing evidence that the sexes are limited independently in both birds (Hannon 1983) and mammals (Redfield et al. 1978, Boonstra and Rodd 1983) indicating that detailed studies of spacing in females may be required to find out how breeding populations are determined. As noted by Brown (1969), if spacing behavior restricts population growth in polygynous or promiscuous birds, there should be an identifiable "surplus" of non-breeding females that is prevented from breeding by social behavior. Female birds are often difficult to observe as they are secretive and do not interact as overtly as do males. Therefore, evidence of surplus females is based mainly on removal experiments (Watson and Jenkins 1968; Bendell et al. 1972; Zwickel 1972, 1980; Hannon 1983; and others). A major assumption underlying such experiments is that replacement birds, which settle on the area where residents have been removed, would not have otherwise settled and bred elsewhere.

Spacing behavior is thought to be important in determining breeding densities of female blue grouse (*Dendragapus obscurus*) (Hannon et al. 1982, Zwickel et al. 1983). Although instances of overt aggression among females of this polygynous species are seldom observed, such interactions are known to occur in spring (Stirling 1968, Hannon 1980, Hannon et al. 1982, Lewis 1984*a*, Bergerud and

Butler 1985) and may bring about a regular pattern of dispersion at this time of year (Bendell and Elliott 1967, Zwickel 1973, Bergerud and Butler 1985). Removal experiments indicate that surplus (i.e., non-breeding) yearling females may exist in both increasing and decreasing populations (Bendell et al. 1972; Zwickel 1972, 1980) and, based on characteristics of reproductive organs, Hannon and Zwickel (1979) identified probable breeders and probable non-breeders among yearling females removed during one such study. Sopuck (1979) and Hannon et al. (1982) monitored spring movements of radio-marked females and concluded that adult females localized on small home ranges about 10 days earlier than yearlings. They suggested that some yearlings were prevented from localizing until adults began to incubate (and could only defend small areas). Hannon et al. (1982) hypothesized that aggression by adult females delayed some yearlings in nesting and could potentially limit the size of the breeding population. Most of the radio-marked yearlings eventually localized and nested, however, and it remained uncertain whether a surplus of non-breeding females usually existed in populations of blue grouse or whether spacing behavior of females normally restricted population growth. Recently, Bergerud and Butler (1985) reported that female blue grouse spaced themselves in a regular pattern and occupied nearly exclusive home ranges in the prelaying period but found no evidence of surplus (non-breeding) hens. In the latter study, females were located by their response to recordings of aggressive calls (termed "cackles"). This census technique might not have been suitable for identifying non-breeding females if such birds are unaggressive and do not vocalize in response to cackles.

Female blue grouse are secretive and difficult to observe so my approach for studying spacing was to radio-mark as many females as possible on a small area and locate them frequently. I hoped to learn how space on breeding range was used by adult and yearling females in spring and how the settlement pattern of adults might influence the subsequent movement and settlement patterns of yearlings. Particularly, I wanted to learn if spacing behavior could prevent some yearlings from breeding and thereby limit population density. The population of blue grouse on Hardwicke Island was declining rapidly from a high density and I had the opportunity to test the generality of the observations made by Sopuck (1979) and Hannon et al. (1982) on a relatively stable population.

8.2 Study Area and Methods

Research was conducted on Hardwicke Island, British Columbia, Canada (50° 25' N, 125° 50' W). The island is situated in the western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965) and supports a variety of successional stages ranging from recently-logged to mature forest greater than 250 years in age.

Early seral stages that follow clear-cut logging are frequently used as breeding habitat by coastal blue grouse and as a site for investigating spatial relationships among females, I chose a 50-ha plot of very open habitat that had been logged less than 10 years previously. On this site, called the "Road Twelve Area" (RD12), I located grouse with a trained pointing dog and used a noosing pole to capture 4 adults and 11 yearling females (Zwickel and Bendell 1967). Each hen was equipped with a radio package similar to that described by Brander (1968). In addition, 4 other yearlings, which had been radio-marked the year before as juveniles, were present on the area. Three other radio-marked adults and 7 other radio-marked yearlings were present within 1.5 km of RD12; they were located frequently to provide additional data on movements and home range sizes. Dates of capture for these grouse varied from 11 April to 8 May ($\bar{X}$ = 21 April ± SE 2 d and were similar to the dates that 4 young grouse radio-marked the previous fall were first observed on RD12 ($\bar{X}$ = 20 April ± 4 d). Thus, the grouse captured on RD12 appeared to be a representative sample of the population of yearlings present in spring. Radio-marked grouse were located on average 18 times before incubation began (about once every 2.2 days), usually by following radio signals to within 10 to 20 m of the bird. Other locations were determined by triangulation from short distances (<100 m).

A census of RD12 began the second week of April 1982 (shortly after migratory adult females first arrived on breeding range) and continued until mid-June when all females were incubating. Non-radioed females were located using a pointing dog, and whenever possible, captured and given a unique combination of colored leg-bands if not previously marked. Parts of the study site were searched daily with a dog to locate and identify non-radioed individuals. Other observers, also accompanied by pointing dogs, routinely worked RD12 as part of an overall census of the 465-ha main study area. Data that they collected made up approximately 10% of all the observations of non-radioed females and were used in the following analyses.

Locations of grouse were plotted on grid maps and, from these data, daily movements, range lengths, and sizes of home ranges were determined. The ***daily movement*** of an individual was the straight-line distance between its location on one day and its location on the following day. Most locations of radio-marked birds were made outside the crepuscular periods (when blue grouse are most active and move the greatest distances). Therefore, I considered locations on consecutive days (although not taken 24 hours apart) were representative of daily movements. ***Size of home range*** was calculated by the minimum area method (Mohr 1947) and ***range length*** was defined as the maximum distance between any 2 locations of an individual for a given time interval. A grouse was said to be localized on an area "if she did not move more than 400 m from the boundary of the area eventually occupied during the period from 10 days before laying (DBL) until the end of laying" (Hannon et al. 1982:688). This definition did not prove useful for blue grouse inhabiting Hardwicke Island which were less mobile than those studied on Vancouver Island. Thus, by an alternate definition, a female was said to be localized when she spent all of her time within the home range she occupied $\leq$10 DBL.

The pattern of dispersion of females on RD12 was analysed in 2 different ways using the nearest neighbor method of Clark and Evans (1954). Centers of activity (Hayne 1949), defined as the mean latitude and longitude coordinates for the sightings of an individual for the period in question, were used in one calculation of nearest-neighbor distances and locations of nest-sites were used in the other. Nests were found for 13 of 21 females that were considered residents of RD12, and for the second analysis, centers of activity were used as approximate location of nests for the remaining 8 females (all non-radioed individuals).

The dispersion of females was further examined as follows. For each observation of a radio-marked yearling on RD12, I calculated the distance to the nearest adult center of activity to find out if yearling females avoided areas occupied by adults. Similar measurements were made for 100 random points which fell on RD12. If distances for yearlings were significantly greater than those expected by chance, this would indicate that yearlings avoided the home ranges of adults. A comparable analysis was undertaken using distance to the nearest adult nest-site (or center of activity if the location of the nest was not known). The methodology was repeated to determine if adults avoided the home ranges of other adults or if yearlings avoided the home ranges of other yearlings. Three time periods were considered: (1) before 1 May, (2) 1 May until the start of incubation (for a given individual), and (3) both periods considered together.

Dates of clutch initiation for brood females whose nests were not found were estimated by backdating as described by Zwickel (1977) and for females whose nests were located as described by Hannon et al. (1982).

8.3 Results

8.3.1 Census of the Study Plot

Fifteen adult females were identified on RD12. Three were seen only once and in all 3 instances were near the edge of the area. They were considered non-residents whose home ranges were mainly outside the plot. Eighteen yearling females were observed; 4 had been previously radio-marked as juveniles, 11 were captured and radio-marked, 1 was captured and color-banded but not radio-marked, and 2 were identified by band combinations but could not be captured. On 2 occasions, a lone unbanded female was observed but not caught. Both sightings occurred within 40 m of each other and were <250 m from the location where an unbanded yearling female was captured on 20 May. After that date, no unbanded females were sighted and it seems likely that all these sightings were of the same female. Nine of the 18 yearling females eventually settled on RD12 (i.e., had at least part of their home range during localization on the study plot). In total, 21 females (12 adults and 9 yearlings) were considered residents of the study site.

A problem with the above data arises if the census was incomplete and all females residing on the study site were not identified. I individually identified 91% of the females encountered during censuses and I believe it unlikely that any resident could be consistently missed throughout spring. A plot of the cumulative number of individuals identified on RD12 against date indicates that all but 2 were identified by 15 May (Figure 8.1). The females that were identified after 15 May included the unbanded yearling (discussed previously) and an adult female captured 3 June. This adult had a brood patch - an indication that she was (or had been) incubating. On 6 June, I found her on a nest outside the study site. Her clutch likely had resulted from renesting as it was incomplete and did not hatch until 2 July (about 2 weeks after the peak of hatching on Hardwicke Island). I suspect that most of her early home range was outside RD12 as no unbanded females had been observed previously in this area.

8.3.2 Breeding Chronology

Female blue grouse that resided on breeding range throughout winter were joined by migratory adults during the first week of April and migratory yearlings about 7 to 10 days later (Hines 1986). Once present on breeding range, females were not as mobile as indicated in previous studies (Sopuck 1979, Hannon et al. 1982). Using the criteria of Hannon et al. (1982), the mean date of localization was 18 April ± SE 3 d for radio-marked adults ($N = 7$) and 20 April ± 2 d for yearling females ($N = 18$) (Mann-Whitney U-test, $P = 0.69$). Thus, according to this definition, most adults and yearlings localized about the same time, shortly after arrival on breeding range. Using the second definition, the mean date of localization was 27 April ± 3 d for adults and 7 May ± 2 d for yearlings. According to this definition, adult females localized on small home ranges earlier than yearlings (Mann-Whitney U-test, $P < 0.01$). The mean date of clutch initiation was 11 May ± 1 d for 7 adults and 19 May ± 1 d for 18 yearlings (Mann-Whitney U-test, $P < 0.01$); on average, adults began to lay eggs 8 days earlier than yearlings.

8.3.3 Movement Patterns Relative to Breeding Chronology

Adult and yearling females were most mobile early in spring, with daily movements of both age classes gradually decreasing until time of laying (Figure 8.2). The regression of daily movements on number of days before laying was significant for both adults ($r = 0.21$, $N = 104$, $P < 0.01$) and yearlings ($r = 0.26$, $N = 114$, $P < 0.01$) but the r^2 values were small (0.05 and 0.07 respectively) indicating that factors other than breeding chronology must have greatly influenced daily movements. A comparison of slopes ($b = 3.9 \pm 1.3$ for adults, $b = 2.8 \pm 1.5$ for yearlings) indicated no difference between groups (t-test, $P = 0.79$). Intercepts for adults (70.2 ± 16.1) and yearlings (126.5 ± 29.3) did not differ (t-test, $P = 0.18$). The overall similarity of regression lines indicated that daily movements of adults and yearlings were alike during any given time period.

Distances of females from their eventual nest-sites decreased greatly throughout the spring (Figure 8.3). Distances from nest-sites were highly correlated with number of days before laying for both adults ($r = 0.45$, $N = 169$, $P < 0.01$) and yearlings ($r = 0.67$, $N = 297$, $P < 0.01$). Slopes of regression lines for adults ($b = 5.5 \pm 0.8$) and yearlings ($b = 10.4 \pm 0.9$) differed significantly ($P < 0.01$) as did intercepts ($a = 55.6 \pm 11.7$ for adults, $a = 92.1 \pm 19.1$ for yearlings, $P < 0.01$). This indicated that yearlings were usually farther from their eventual nest-sites early in spring than were adults but this distance decreased at a more rapid rate for yearlings than for adults as the time of nesting approached. During the period >10 DBL adults were found within 100 m of their eventual nest-site in 25% of all sightings and in 51% of the sightings ≤10 DBL. In contrast to adults, yearlings were farther from their nest-sites early in spring. During the period >10 DBL, only 12% of the observations of yearlings were within 100 m of their nest-sites and only 38% were within 200 m of their nests. Ten days or less before laying, yearlings were found within 100 m of the nest in 58% of all sightings and thus, were similar to adults in this regard (Figure 8.4).

8.3.4 Sizes of Home Ranges and Range Lengths

Sample sizes were too small for accurate measurement of home ranges or range lengths for each 10-day interval and instead, 3 different periods were considered: 1) >10 DBL, 2) ≤10 DBL, and 3) both periods combined. The second interval (≤10 DBL) is most apt to be the period when female blue grouse are territorial as it is at this time that aggressive calls are heard most frequently (Hannon 1980, Hannon et al. 1982).

Overall home ranges of yearlings were larger than those of adults (Table 8.1) and during the period >10 DBL, yearling home ranges were more than twice the size of those of adults. This difference was not significant, however, probably because of small sample sizes. During the period ≤10 DBL, adults and yearlings occupied home ranges of similar size.

Variations in range length followed the same general pattern as variations in size of home range. Overall range lengths of yearlings were larger than those of adults (Table 8.1) but this relationship did not hold for the period >10 DBL (again probably because of small sample sizes). For the period ≤10 DBL, average range lengths of adults and yearlings were similar.

8.3.5 Spacing Patterns

During April and May 1982, I used a pointing dog to thoroughly search the area where 108 females were sighted. In only 4 instances (involving a total of 9 grouse) were females found together suggesting that females normally avoided each other in spring or, at least, were not social.

Home ranges of females covered virtually all of the study plot during spring and total home ranges of adults and yearlings overlapped greatly (Table 8.2). The degree of overlap after 1 May was much less, however (Figure 8.5).

The locations of nest-sites (or centers of activity if locations of nest-sites were not known) are shown in Figure 8.6. Analysis of these data by the nearest neighbor method (Clark and Evans 1954) indicated that neither nest-sites nor centers of activity of adults, yearlings, or adults and yearlings considered together were regular spaced (Table 8.3). Sample sizes were small, however, and the Clark-Evans test may not have been appropriate under these circumstances.

Another way of looking at spatial patterns of adult and yearling females is to measure distances of yearlings from the nearest adult home range and compare these distances to those expected by chance. On RD12, 100 random points fell a median distance of 113 m from the nearest nest-site or center of activity of an adult female. This was similar to the median of 97 m that 100 sightings of yearlings were from centers of activity of adults (Mann-Whitney U-test, $P = 0.86$) during spring. Comparisons for the period when adult females are apt to be more aggressive (after 1 May) gave similar results. Further comparisons provided little evidence that females (of either age) strongly avoided the nest-sites or centers of activity of other females (Table 8.4).

8.3.6 Proportion of Yearling Females that Nested

Eleven of the 15 radio-marked yearling females sighted on RD12 were known to nest. Nests were not found for 4 of the 15 yearlings; one lost its radio-package, another was killed by a predator, and a third had a faulty transmitter and could not be tracked. The other radio-marked female wandered during the breeding season and apparently did not nest. In total, 11 of 12 yearling females that could be followed throughout the breeding season eventually nested. A similar pattern was noted for yearlings living elsewhere on Hardwicke Island where 8 of 8 females that had been radio-marked the previous year nested. In short, there was little evidence of non-breeding yearling females this year.

8.4 Discussion

On Hardwicke Island, female blue grouse showed patterns of movement and settlement in spring that were *qualitatively* similar to those of females studied on Vancouver Island (Sopuck 1979, Hannon et al. 1982). Adult females arrived back on breeding range before yearlings and, early in the breeding season, moved about on home ranges averaging 7 ha, spending much of their time within 200 m of their eventual nests. During the period that lasted from 10 days prelaying until the end of laying, adult females localized on small home ranges of 2 or 3 ha and spent about half of their time within 100 m of their nests. Thus, the radius around the nest that might have been defended by adult females was about 100 m.

Migrating yearling females arrived on breeding range a week or more after adults. Yearlings moved more widely during the early part of the breeding season than adults but most eventually localized on breeding range. The timing of localization of yearlings relative to that of adults was difficult to ascertain as it depended largely on how localization was defined. Following the criteria of localization given by Hannon et al. (1982), most yearlings and adults were already localized when first sighted on breeding range. This occurred about 20 DBL for adults and nearly 30 DBL for yearlings. According to the second definition, adults localized some 11 days before yearlings and the mean date of localization for adults was 14 DBL whereas that of yearlings averaged 10 DBL. Early in spring, home ranges of yearlings were about twice as large as those of adults and distances from nest-sites for yearlings much greater than for adults. About the time of nesting, home range sizes and movement patterns of yearlings closely resembled those of adults. In general then, adult and yearling movement patterns differed mainly early in spring when yearlings wandered more widely than adults.

Hannon et al. (1982) hypothesized that adults might prevent yearlings from localizing early in spring and this could account for differences in the patterns of movement and settlement of the 2 age classes. They suggested that after adults began to incubate (and could only defend small areas), yearlings were able to settle. My data indicate that the relationship that one draws between timing of localization of yearlings and adults depends largely on how one defines localization and it is clear that less arbitrary definitions of localization are required before the influences of spacing behavior on recruitment by yearlings can be assessed. At present, alternate explanations of late breeding by yearlings are equally tenable. For example, yearlings arrive on breeding range 7 to 10 days later than do adults so at least part of the differences in time of breeding might be attributed to later arrival dates of yearlings. One might also argue that yearlings wander in order to sample different habitats before they settle (Hannon et al. 1982). Therefore, the relationship between late breeding in yearlings and aggressive behavior of adults remains unclear.

Home ranges of adults overlapped greatly during the early spring and most yearlings wandered about the known home ranges of several adults. Neither nest-sites or centers of activity of adults tended to be regularly spaced on breeding range and adult home ranges were not exclusive of those of other adults even during the period of localization. Further, I could not detect a regular distribution pattern for yearlings, or for yearlings and adults considered together. Comparisons of distances of random points and distances of yearling females from nest-sites or centers of activity of adult females provided no evidence that yearlings avoided areas occupied by adults.

The apparent lack of evenness or regularity in the overall spacing pattern of females has several possible explanations. One possibility is that part of RD12 was suboptimal breeding habitat thus bringing about the clumping of females within areas of suitable habitat (spacing patterns of females within areas of suitable habitat might, however, still be regular). Second, population densities on Hardwicke Island in 1982 were relatively low compared to those of previous years and perhaps under these conditions some suitable habitats were not being used by breeding females. Third, it is possible that the spacing mechanism of female blue grouse is too weak to bring about a regular distribution of home ranges. Finally, the number of observations of some individuals was small and perhaps regular patterns were not detected because of small sample sizes. The relative importance of each of these factors cannot be determined at present as the habitat preferences of female blue grouse on breeding range, or the way in which spacing might influence the use of good and poor habitats, are not well understood. In any event, the tendency for females to be randomly distributed and the high degree of overlap of home ranges suggests that spacing system of females is far less rigorous than that of males which tend to show a more regular distribution and very little overlap of territories (Bendell and Elliot 1967, Lewis 1984*b*). The fact that females were seldom seen together in spring suggests that some sort of spacing occurred -- perhaps it had a dynamic quality to it that could not be measured in the present study.

Watson and Moss (1970) presented several criteria that, if met, would provide suitable evidence that spacing behavior limited population density. Their most important criterion was—that there must be a "substantial" surplus of non-breeders that were excluded behaviorally from acquiring a place to breed. This requirement was not met in the present study as most yearling females nested. Thus, under conditions of reduced population density there appeared to be adequate space available for yearling females and these yearlings were able to find this space. Similarly, Sopuck (1979) studied recruitment of radio-marked yearling females on Vancouver Island and found that 87-96% of the yearling females nested. Sopuck (1979) indicated that production of young (reproductive success) in the years that immediately preceded his work may have been unusually low; and hence, the surplus of non-breeding yearlings was much lower than usual.

The results of studies of radio-marked grouse somewhat contradict earlier removal experiments (Bendell et al. 1972; Zwickel 1972, 1980) which suggested a relatively large surplus of non-breeding yearlings. Studies of radio-marked grouse may have followed years of low reproductive success (Sopuck 1979) or dealt with declining populations (this study) and may not be representative of what happens when populations are higher or more stable. Another possibility is that removal experiments exaggerate the size of the surplus. For example, only 9 of 18 yearlings observed on RD12 eventually settled on the plot; the others nested elsewhere. Presumably, had I removed adults from RD12 early in spring, many of these yearlings would have localized and settled there and hence been identified as "surplus" in a removal experiment. Conducting a removal study later in spring would indicate few if any surplus animals.

Although the present study has a number of shortcomings (including the small number of radio-marked birds and the infrequency with which both radioed and non-radioed grouse could be located), the data indicate that home ranges of females are not exclusive and suggest that, under conditions of lowered population density, the pattern of spacing of females is not rigid. Thus, under the conditions of this study (i.e. that of a decreasing population that was less than half the maximum density previously recorded on the main study area), spacing behavior seemed to have a limited effect on numbers of breeding females. At such times factors which might influence the availability of potential recruits and hence, the size of the breeding population are reproductive success in the previous summer and subsequent survival of young over winter.

Further studies of spacing behavior should involve marking all females on a given area and monitoring them at frequent intervals to determine time-specific patterns of movement and dispersion. Attempts to evaluate how females use space within their home ranges and the important features or resources in these home ranges that might be defended also deserve investigation. The infrequency with which aggressive interactions are observed indicates that spacing of female blue grouse might occur by avoidance rather than direct aggression. For such a spacing mechanism to operate, there must be significant benefits accruing to the female that avoids the area already occupied by another female. Thus, to understand the mechanism whereby females space themselves, one must identify the nature of such benefits.

8.5 Summary

Spring movements and spacing patterns of female blue grouse were studied through radio-tracking and reobservation of color-banded birds. Yearling females were more mobile than adults in early spring and nested about 8 days later on average than adults. Both yearlings and adults restricted their movements to home ranges that averaged 2-3 ha $\leq$10 days before the onset of laying. Overlap of home ranges was greatest in the early spring (before 1 May) but decreased as the breeding season advanced. Nearest neighbor analysis indicated that nest-sites or centers of activity were randomly distributed on a 50-ha study plot. Similar analyses based on the distance of random points and females from the nearest nest or activity center yielded similar results. Despite this, females were seldom seen together indicating some sort of spacing may have occurred. Most yearling females nested suggesting that spacing behavior did not limit numbers under conditions of a declining population.

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TABLE 8.1. Mean size (± SE) of spring home ranges (ha) and range lengths (m) of radio-marked female blue grouse on Hardwicke Island, British Columbia. Sample sizes are in parentheses.

Parameter	Adults	Yearlings	*P*[a]
Home range (ha)			
>10 DBL[b]	7.4 ± 1.6 (4)	13.6 ± 2.4 (17)	0.28
≤10 DBL	2.8 ± 0.5 (7)	2.7 ± 0.4 (13)	0.78
Both periods	6.6 ± 1.3 (7)	16.1 ± 2.5 (18)	0.01
Range length (m)			
>10 DBL	511 ± 112 (4)	759 ± 94 (17)	0.15
≤10 DBL	318 ± 33 (7)	280 ± 26 (13)	0.32
Both periods	450 ± 68 (7)	764 ± 85 (18)	0.02

[a] Mann-Whitney U-test.

[b] Days before laying.

TABLE 8.2. Overlap of spring home ranges of radio-marked female blue grouse on Hardwicke Island, British Columbia.

Age and sex	% of home range ± SE (*N*) shared
Adult females	
with adult females	50 ± 9 (11)
with yearling females	73 ± 11 (11)
with adults and yearlings	84 ± 5 (11)
Yearling females	
with adult females	46 ± 9 (14)
with yearling females	82 ± 6 (14)
with adults and yearlings	89 ± 4 (14)
All females	87 ± 3 (25)

TABLE 8.3. Nearest-neighbor analyses for nest-sites and centers of activity of adult[c] and yearling females on RD12, Hardwicke Island, British Columbia, May 1982.

Parameter	*N*[a]	*R*	*P*[b]
Activity centers - adult females	12	1.08	>0.10
Nest-sites - adult females	10	1.30	0.07
Activity centers - yearling females	7	0.99	>0.10
Nest-sites - yearling females	8	1.22	>0.10
Activity centers - all females	19	0.93	>0.10
Nest-sites - all females	18	0.98	>0.10

[a] Number of nests or centers of activity on RD12 study site.

[b] Statistical comparisons are based on the nearest-neighbor method of Clark and Evans (1954). *R*-values significantly greater than 1.00 indicate a regular distribution.

[c] Center of activity used as approximation of nest-site when location of nest unknown.

TABLE 8.4. Spacing patterns of adult and yearling female blue grouse as indicated by distances (m) of random points and sightings of females to the nearest nest or center of activity of a female.

Distance category (m)	Period	Median	Range	N	P^{a}
Random points to adult centers of activity	–	113	0 - 220	100	–
Yearling sightings to adult centers of activity	All spring[b]	97	10 - 260	100	0.86
Yearling sightings to adult centers of activity	May	96	10 - 240	67	0.48
Random points to adult nests[c]	–	102	0 - 220	100	–
Yearling sightings to adult nests	All spring	96	20 - 260	100	0.72
Yearling sightings to adult nests	May	96	20 - 240	67	0.93
Random points to adult centers of activity	–	113	0 - 220	100	–
Adult sightings to adult centers of activity	All spring	98	20 - 400	112	0.23
Adult sightings to adult centers of activity	May	106	20 - 400	72	0.75
Random points to adult nests	–	102	0 - 220	100	–
Adult sightings to adult nests	All spring	106	10 - 410	112	0.69
Adult sightings to adult nests	May	111	10 - 410	72	0.52

continued

TABLE 8.4 continued.

Distance category (m)	Period	Median	Range	N	P[a]
Random points to yearling centers of activity	–	145	10 - 350	100	–
Yearling sightings to yearling centers of activity	All spring	157	20 - 380	100	0.42
Yearling sightings to yearling centers of activity	May	149	20 - 360	67	0.91
Random points to nearest yearling nests	–	120	10 - 290	100	–
Yearling sightings to nearest yearling nests	All spring	128	10 - 360	100	0.42
Yearling sightings to nearest yearling nests	May	133	20 - 360	67	0.15

[a] Mann-Whitney U-test comparing distances of random points and distances of sightings from nearest nest or center of activity.

[b] From time of arrival on breeding range until start of incubation.

[c] Center of activity used when location of nest unknown.

FIGURE 8.1. Cumulative frequency distribution of dates on which individual females were first identified on the RD12 study site in 1982.

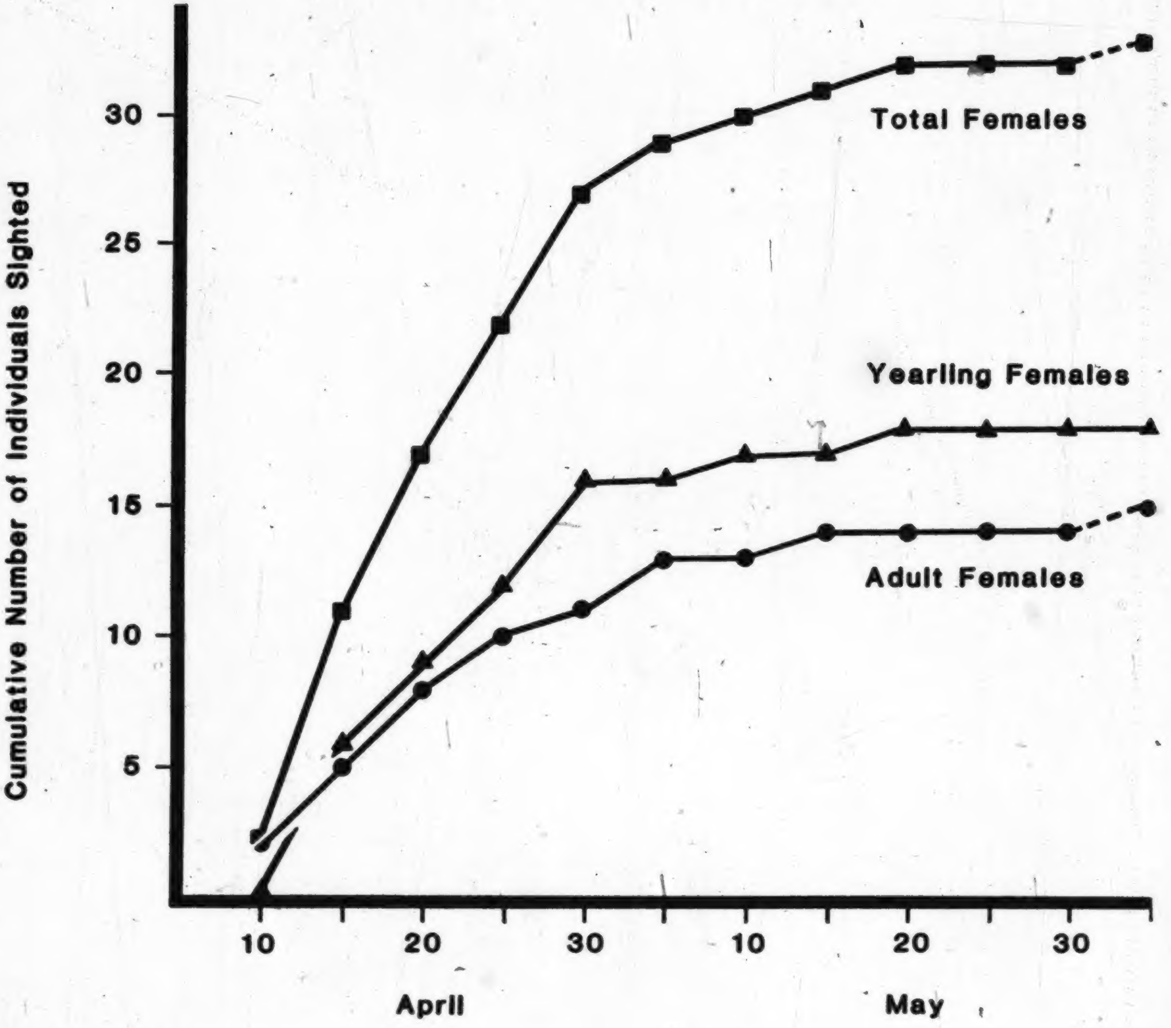

Cumulative Number of Individuals Sighted
5
10
15
20
25
30
10
20
30
10
20
30
April
May
Total Females
Yearling Females
Adult Females

FIGURE 8.2. Daily movements (m) of adult and yearling blue grouse in relation to breeding chronology (number of days before laying). Sample sizes are indicated for each period.

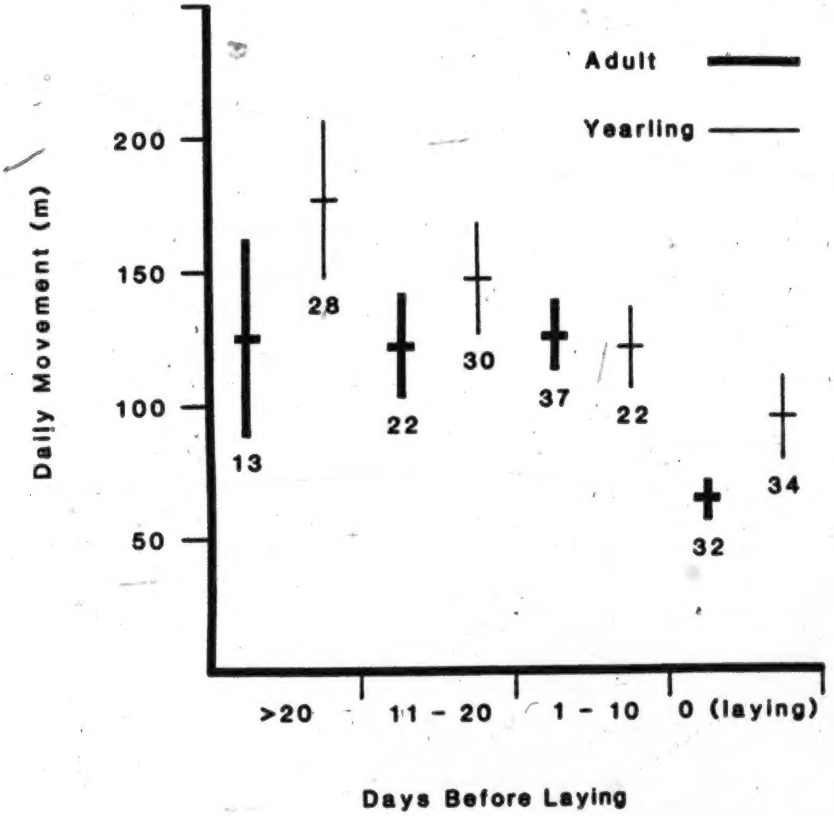

Adult
Yearling
200
150
100
50
Daily Movement (m)
13
28
22
30
37
22
32
34
>20
11 - 20
1 - 10
0 (laying)
Days Before Laying

FIGURE 8.3. Distances (m) of adult and yearling females from their nest-sites in relation to breeding chronology (number of days before laying). Sample sizes are indicated for each period.

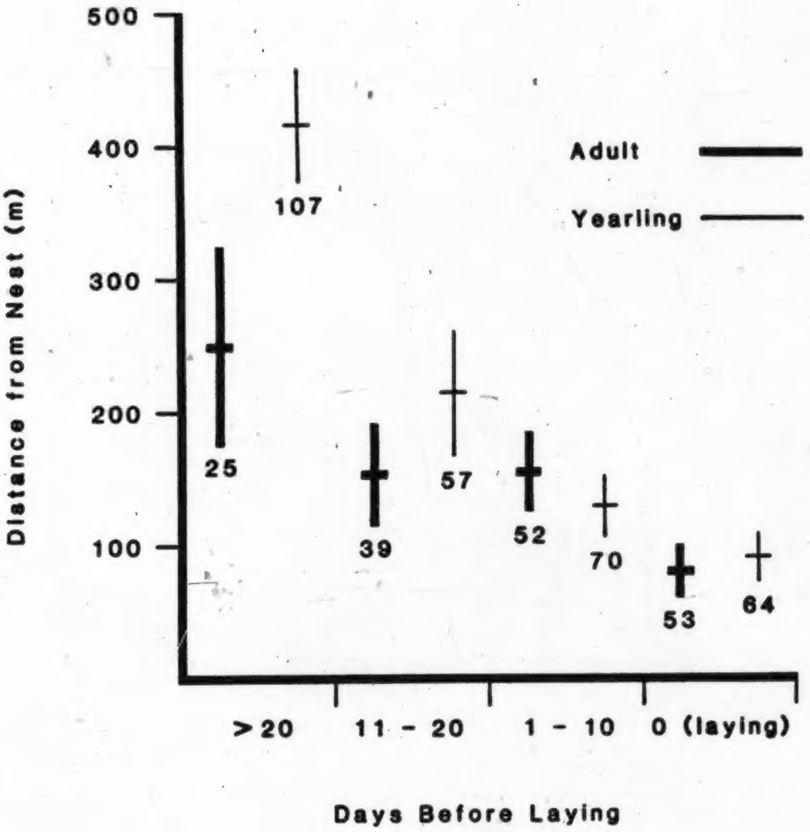

500
400
300
200
100
Distance from Nest (m)
107
25
57
39
52
70
53
64
Adult
Yearling
> 20
11 - 20
1 - 10
0 (laying)
Days Before Laying

FIGURE 8.4. Distances (m) of adult and yearling females from their nest-sites $\leq$10 days before laying and >10 days before laying. Sample sizes are indicated for each period.

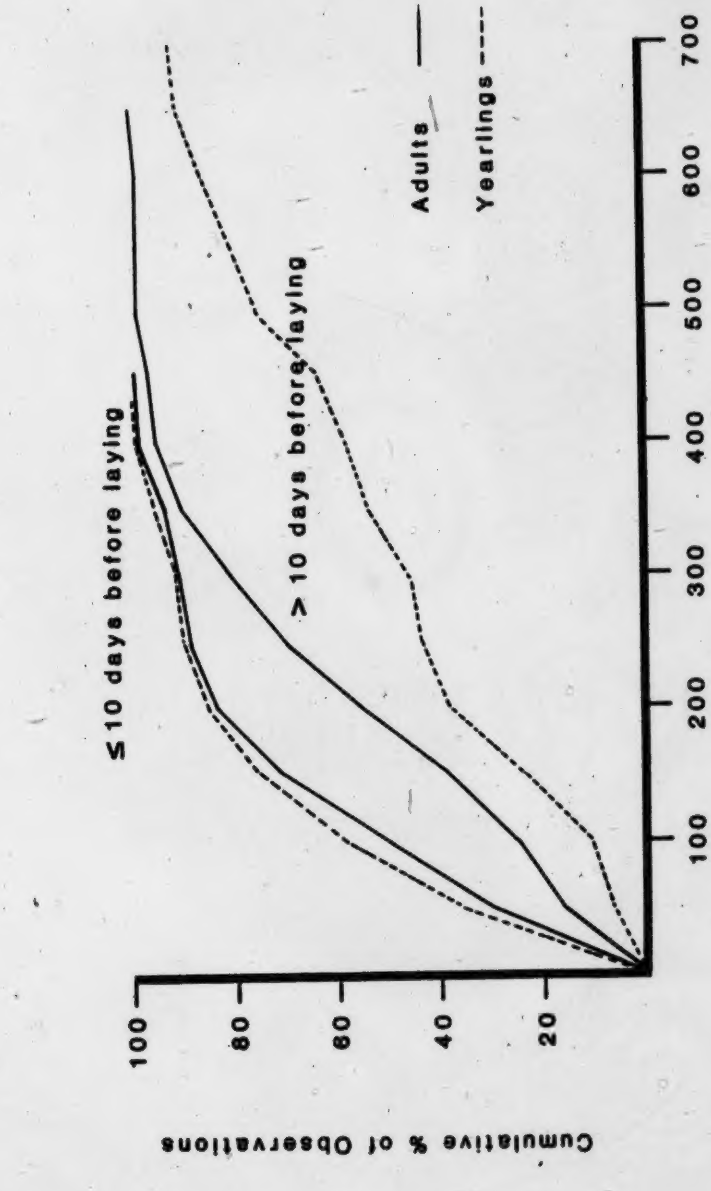

≤ 10 days before laying
> 10 days before laying
Adults
Yearlings
Cumulative % of Observations
100
80
60
40
20
100
200
300
400
500
600
700
Distance from Nest (m)

FIGURE 8.5. Overlap of home ranges of female blue grouse on RD12 after 1 May. The broken line indicates the boundary of the study area. An adult (A) and a yearling (Y), each sighted only once after 1 May, are indicated.

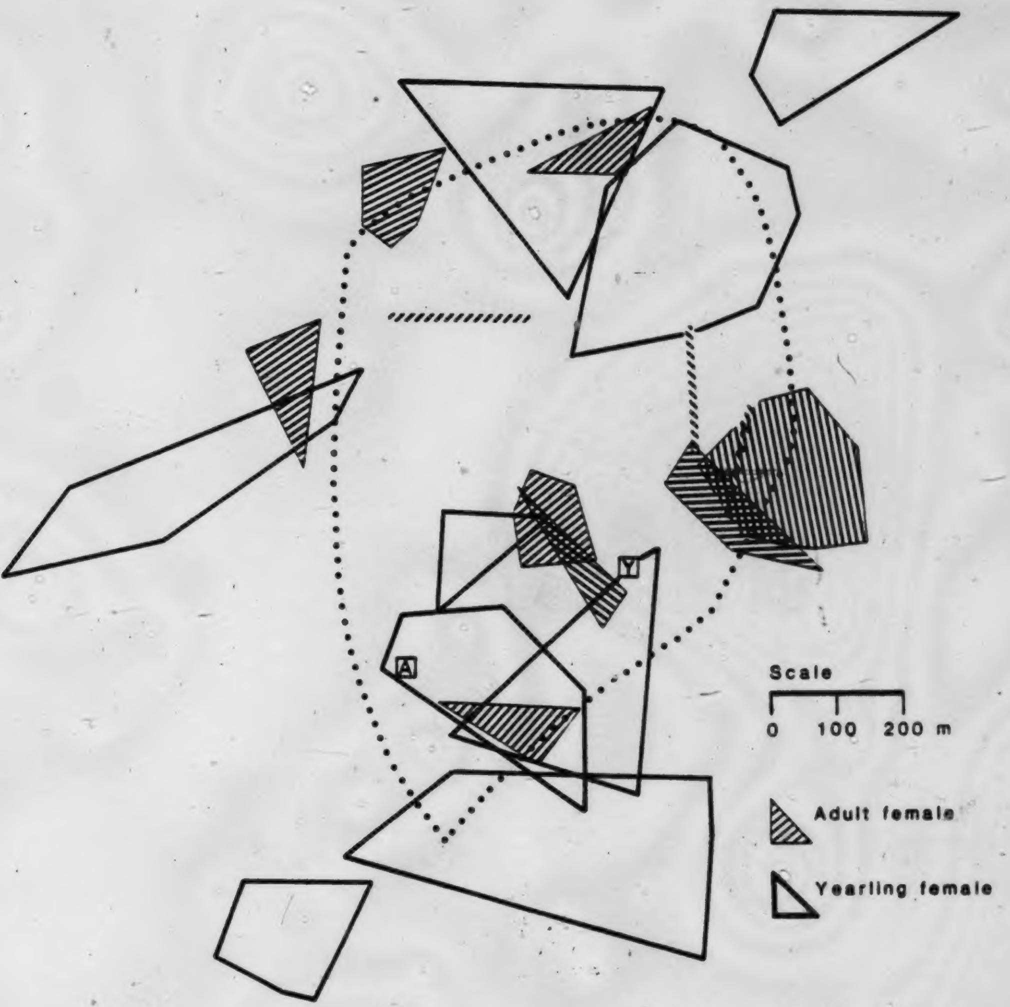
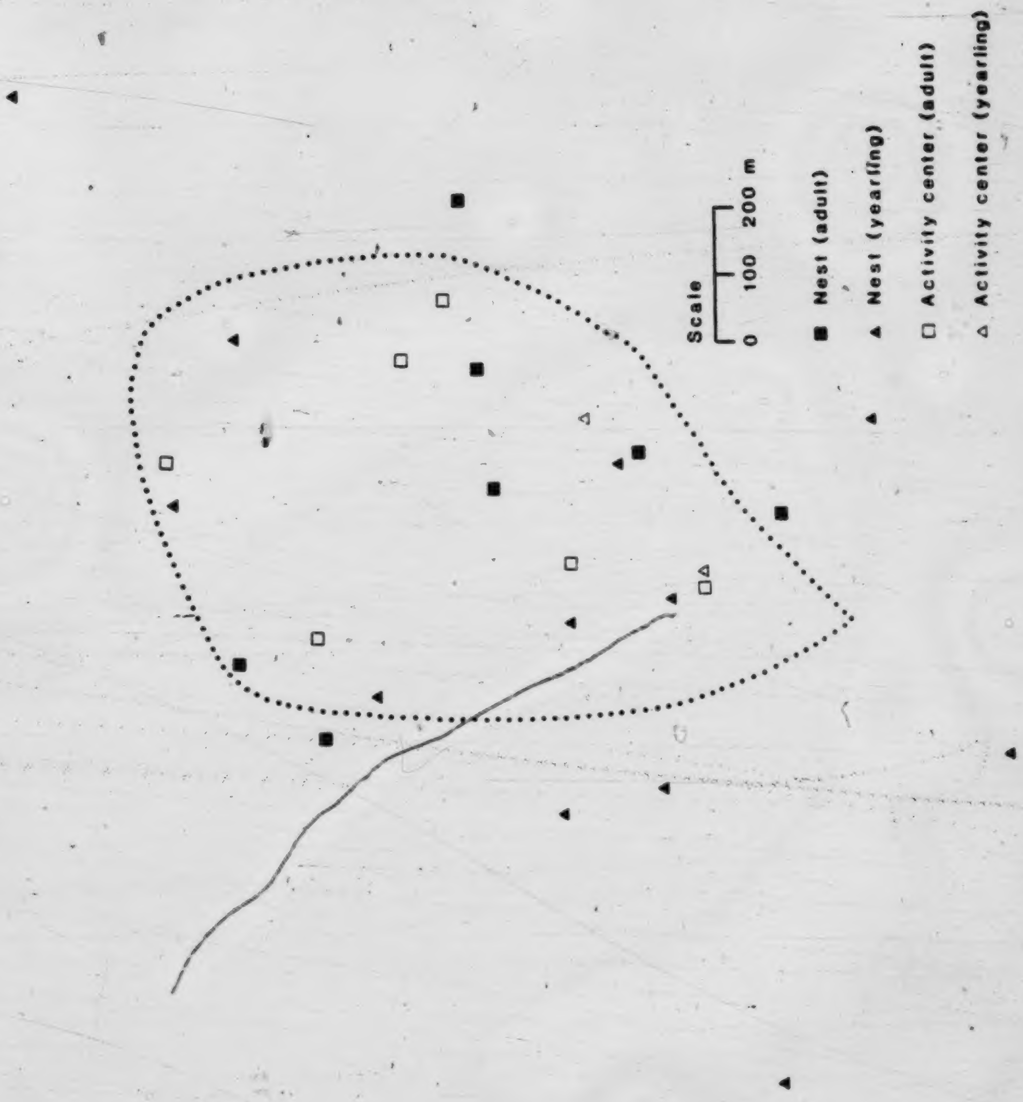

Y
A
Scale
0
100
200 m
Adult female
Yearling female

FIGURE 8.6. Locations of nests and centers of activity (after 1 May) of adult and yearling female blue grouse on RD12. The broken line indicates the boundary of the study area.


Scale
0 100 200 m
■ Nest (adult)
▲ Nest (yearling)
☐ Activity center (adult)
△ Activity center (yearling)

9. CONCLUDING DISCUSSION

A variety of hypotheses have been invoked to explain how animal populations are limited or regulated. They can be divided into 2 general schools of thought. According to the *extrinsic school*, factors from outside the population such as climate, predators, disease, and food supply usually prevent unlimited population growth. In contrast, members of the *intrinsic school* believe that animal populations are normally limited by some form of behavior that prevents some individuals from entering the breeding population or causes increased mortality or lower reproduction when population densities are higher. Other biologists take a more holistic view of population ecology and suggest that many factors (both intrinsic and extrinsic) are involved in population limitation. Such *multifactorial hypotheses* have been rejected by some observers as being untestable but, as noted by Hilborn and Stearns (1982), such need not be the case. In fact, failure to consider additional factors that contribute to the overall variance in the subject under study may result in rejection of the most important causal factor.

Bakker (1964), Chitty (1967), Zwickel and Bendell (1972), Krebs (1978) and others have observed that it is useful to recognize the difference between factors that set a general limit to the number of animals in a given area and those involved in the mechanism of numerical change or maintenance of relative stability on an area.[4] The former are sometimes referred to as *ultimate limiting factors*, the latter as *proximate limiting factors* (Moss et al. 1982); they need not be the same. Population densities may differ greatly between areas because resources (ultimate limiting factors) are abundant in one area but not in the other whereas annual changes in population size on any given area result from changes in intensity of predation, territorial defence, weather, or some other proximate limiting factor. For example, the ability of different moors in Scotland to support red grouse (*Lagopus lagopus scoticus*) is influenced by the quality of the food supply (Moss 1969). The proximate mechanism involved in annual variations in numbers is thought to be spacing behavior which may (Watson and Moss 1972) or may not be (Watson and Moss 1980) related to food quality.

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[4] These authorities use somewhat different terminology but share a common viewpoint: variations in population densities among areas may have different causes than annual changes in population density within a given area.

Factors that ultimately limit blue grouse populations are not well understood although they seem to be related to the availability of open areas for breeding (Niederleitner 1982, Bendell and Zwickel 1985). For Hardwicke Island, I have no quantitative information which would show if or how habitat changes have influenced blue grouse numbers during the 4 years of study. Populations of blue grouse on nearby Vancouver Island increased or remained stable throughout longer periods of plant succession (Zwickel and Bendell 1972, Zwickel et al. 1983) and it seems unlikely that plant succession was instrumental in the decline on Hardwicke Island. Thus, in the following discussion, I address the proximate factors involved in the mechanism of population change and probably not the ultimate factors that set the overall carrying capacity of the area.

Essentially, I set out to test 2 hypotheses of population limitation. One hypothesis was that an intrinsic factor (social behavior in spring) limited recruitment and restricted population growth; the other hypothesis was that mortality during autumn and winter limited recruitment. My findings on dispersal, recruitment, over-winter mortality, social organization, habitat use, and spacing of females in spring as they relate to these 2 hypotheses, are discussed below.

9.1 Social Organization and Habitat Selection in Winter

On Hardwicke Island, most blue grouse wintered alone or in small groups of 2 or 3. Grouse inhabited a broad range of successional stages in which western hemlock was the dominant plant. Hemlock made up about two thirds of the tree cover along vegetation transects, was the dominant tree at 94% of the locations where grouse were observed in winter, and comprised much of the winter diet of blue grouse. It is unlikely that quantity of food was in short supply because hemlock and Douglas-fir (the other major food) were very abundant. All evidence suggests that grouse maintain or put on weight during winter and it is probable that food quality was adequate as well. The above evidence is circumstantial, however, and the role of food in the over-winter survival of blue grouse requires further investigation.

Was the heavy mortality of young grouse induced by some form of spacing or dominance behavior during autumn and winter? I saw little evidence of social interactions among grouse and think it unlikely that such a large number of deaths were socially induced. Studies of blue grouse in the aviary (Stirling 1968) also indicate that aggression is low outside the breeding season but subtle forms of behavior, which are not readily observed, could occur and the behavior of grouse during the non-breeding season and its influence on recruitment deserves further study.

9.2 Dispersal

Dispersal in blue grouse was not a simple, single-stage process and involved at least 3 different kinds of movements whose causes were difficult to evaluate. In autumn, young grouse migrated to winter range and in spring undertook another migration to a potential breeding area. Once having arrived on breeding range, yearlings wandered in search of potential areas in which to settle. None of the 3 types of movements (autumn migration, spring migration, or movements on breeding range) was significantly correlated with dispersal distance when considered separately but multiple regression analysis suggested that grouse that dispersed longer distances were those that moved longer distances in fall and then settled in spring near where they had wintered.

Dispersal was not associated with a specific time of year when peak aggression presumably occurred nor did dispersal distances vary annually with changes in population density. On average, grouse that dispersed longer distances fared as well, in terms of survival and reproductive success, as grouse that moved shorter distances. Thus, emigrants from the study area were immigrants to other areas. This observation has an important implication for limitation of breeding populations because, if dispersers settle successfully, emigration may influence local densities but have little effect on overall population size (Keppie 1979). If the results from Hardwicke Island have any generality, I suggest that when breeding densities are limited by spacing behavior, non-breeding rather than dispersal (and subsequent death or poor reproductive success) is the typical fate of a surplus female blue grouse.

Watson and Moss (1979) and Watson et al. (1984) hypothesized that dispersal was involved in cyclic changes in grouse numbers and Moss et al. (1982) suggested that dispersal was important in the self-regulation of stable populations. It is difficult to visualize how dispersal might have been involved in the population decline on Hardwicke Island because dispersal distances were not density-dependent, dispersal did not vary annually, and dispersers and non-dispersers had similar rates of survival and breeding. Therefore, I conclude that factors other than dispersal caused the population to decline.

One potential bias associated with using islands as study areas is the possibility of a "fence" effect (Krebs et al. 1969, Boonstra and Krebs 1977, Tamarin 1977, and others). When populations of small mammals are fenced and prevented from dispersing, numbers may grow to unprecedented levels, the population over-eats its food supply, and subsequently crashes. Theoretically, similar events also might occur on small islands. To my knowledge, fence effects have been shown to take place only under extremely unusual conditions (very small fenced plots) and have never been reported for birds. For these reasons, I believe it unlikely that a fence effect occurred on an area as large as Hardwicke Island.

The role of dispersal in regulating populations has been widely acclaimed but, despite this, there is surprisingly little known about the causes or consequences of dispersal. I suggest that far too much has been attributed to dispersal than is warranted by available information.

9.3 Dispersion of Females in Spring

Hannon et al. (1982) developed the following model of how social interactions might affect breeding densities of female blue grouse. In spring, adult females arrive on breeding range before yearling females and localize on or near the home range they had occupied the previous year. From 10 days before laying until the end of laying, adult females are aggressive and defend at least part of their home range against other females. Yearlings arrive on breeding range 7 to 10 days after adults and wander until they find vacant areas in which to settle. On average, about half of the breeding population has died since the previous spring and some yearlings quickly find vacant space in which to settle. Other yearlings wander, are displaced by localized hens, and only settle when adults begin to incubate and are no longer defending large areas. Still other yearlings do not find places to settle in time to breed; they comprise the surplus or floater population.

My data indicate that female blue grouse were not strongly territorial in the sense of defending exclusive areas or spacing themselves in a regular pattern on breeding range. Despite this, females were solitary in spring indicating that some sort of spacing may have occurred. The apparent lack of rigidity in the territorial system suggests that female spacing might be manifested as a "moving territory" (Jenkins 1944) or "individual distance" (Conder 1949) rather than as an "exclusive area" (Pitelka 1959). If this is so, spacing of females might have a dynamic temporal aspect to it that was not readily detected by methods used in the present study. Investigations in which all females are radio-marked and located frequently may be needed to clarify this matter.

The lack of rigidity in the spacing system has an important implication for population regulation. The number of young grouse surviving until spring might greatly influence recruitment under these circumstances because of (1) synchronous settlement of numerous recruits when adult mortality is great, and (2) intrusion pressure when the number of potential recruits is high.

The effect of synchronous settlement on recruitment was observed by Tompa (1964, 1971) who found that many more song sparrows (*Melospiza melodia*) were able to settle in a year following "catastrophic" mortality of adults than would normally be expected. He attributed this to a disruption in the social system which allowed many young birds to settle synchronously and occupy smaller territories than usual, a view that Knapton and Krebs (1974) confirmed experimentally. Annual mortality rates of female blue grouse (40-50%) are not greatly different from the 54% reported for song sparrows during the year of catastrophic mortality (Tompa 1964:42), consequently synchronous settlement could influence recruitment of female blue grouse during most years.

Intrusion pressures, determined by the number of potential recruits alive in spring, may also influence size of the breeding population (Patterson 1980, Smith et al. 1980). If all (or at least a constant proportion) of the potential recruits enter the breeding population each spring, the relationship between the number of potential recruits surviving over winter and subsequent recruitment should be linear (Figure 9.1, Line A) (Davies 1978, Patterson 1980). If recruitment is behaviorally limited, the relationship should appear as in Line B -- some animals have greater difficulty in entering the breeding population as density increases. Patterson (1980) suggested that an intermediate situation (Line C) was most probable; it becomes more and more difficult for an individual to enter the breeding population as competition for space increases but the absolute limit for recruitment is usually not reached. This situation falls between the predictions of Lack's (1954, 1966) and Wynne-Edwards' (1962) hypotheses.

Although female blue grouse may not show territoriality in the classical sense, their behavior could still have a profound effect on population density. For Hardwicke Island, this is substantiated by the fact that most yearling females nested during 1982 and 1983 when population levels were low but proportionally fewer nested when population density was higher in 1980 and 1981. Thus, some yearling females may have been prevented from breeding when population densities were high.

9.4 Survival Over Winter

Survival of young grouse from late summer until the following spring was poor and was likely involved in the population decline on Hardwicke Island. What was the cause of this poor survival? One possibility, that radio-marking caused higher mortality of juveniles, seems unlikely as there were no detectable differences in the survival, movements, or reproduction of radioed and non-radioed grouse (Appendix 1). Deaths of many young grouse occurred on summer range about or shortly after the time broods were breaking up. After autumn migration, mortality was lower and remained fairly constant throughout winter. Predation by raptors, most notably northern goshawks (*Accipiter gentilis*), was the proximate cause of many deaths and, for reasons mentioned previously, it is improbable that either social behavior or malnutrition predisposed a large number of individuals to predation. High rates of predation seemed to be involved in the poor survival of juveniles but unfortunately, I have little information on the numbers or food habits of predators on Hardwicke Island.

9.5 Production of Young and Recruitment

Poor reproductive success or poor survival of young in summer may have caused the low level of recruitment on Hardwicke Island as the number of young produced on the study area in one year was correlated with the number of recruits in the following spring. Similar occurrences have been reported for ptarmigan (*Lagopus* spp.) (Jenkins et al. 1963, Bergerud 1970, Weeden and Theberge 1972; Myrberget 1972, 1984) and attributed to annual variations in rates of nest predation or survival of young after hatching. I believe that this result is not consistent with the spacing behavior or the over-winter mortality hypotheses as proposed for blue grouse. Both hypotheses predict that far more young are produced annually than are needed to replace dying adults and that the number of recruits should be unrelated to the number of young produced in the previous year. The factors which determine production of young blue grouse are not well understood, but the influence of prehatching factors on subsequent survival of chicks particularly should be investigated as these are known to influence survival (Zwickel and Bendell 1967).

9.6 What Determines Recruitment in Populations of Blue Grouse?

The data for blue grouse populations on Hardwicke Island do not clearly support or refute either Lack's or Wynne-Edwards' hypotheses of population limitation. This might reflect inadequacies in the set of data used to test the hypotheses or shortcomings in the theory itself. Although the data are less than perfect, this study is one of the few attempts to document losses of potential recruits through death, dispersal or failure to breed for an avian population. I feel that the failure to clearly support or refute either hypothesis is not because of limitations in the data but because of short-comings in single-factor thinking. The hypotheses were set out as mutually exclusive alternatives in the limitation of populations but perhaps they should be viewed as complementary. My data suggest that populations in any given year are likely influenced by previous reproductive success, survival over winter, and spacing behavior in spring. In turn, these parameters are likely the product of a number of environmental and biotic factors.

Overall, there was inadequate recruitment to replace older females that died from one year to the next and, as a consequence, the population of blue grouse on Hardwicke Island declined. Low production of young coupled with high mortality of these juveniles appeared to cause this poor recruitment. There was however, evidence of non-breeding by yearling females when densities were high suggesting that spacing behavior impeded population growth under these circumstances. As argued previously, even when some "surplus" grouse are prevented from breeding, the number of potential recruits alive in spring (determined by production of young and their subsequent survival over winter) is apt to influence subsequent recruitment because of intrusion pressure.

How do these data compare to those collected for other populations of blue grouse? In Table 9.1, I have attempted to summarize some of the pertinent demographic information on populations of blue grouse (studied for 3 years or longer) and determine if any general demographic trends are associated with population change or stability. Populations have been ranked from rapidly declining to increasing (based on average percentage change in the number of territorial males) so that non-parametric correlations between demographic parameters and rate of population growth could be performed. Although methodology, intensity of field work, and characteristics of the study areas vary between studies (and undoubtedly somewhat influence the results), I believe a cautious comparison of these data is valid.

First, note that the annual survival rates for adults and yearlings did not vary systematically with population trends (Table 9.2). Similarly, nesting success had no obvious influence on population growth -- the highest rates of nesting success were actually found in declining populations. Although average clutch size was smallest in the rapidly declining population on Hardwicke Island, clutches were large in the declining population studied by Boag (1966) in Alberta indicating that small clutches were not necessary for the population to decline. Average brood size was largest in the increasing population studied by Redfield (1975) but large broods were associated with the declining population studied by Boag (1966) and the smallest broods were found in relatively stable populations at Comox Burn and the Quinsam Lakes areas on Vancouver Island. Thus, survival of young throughout summer (as indicated by brood sizes) was not consistently correlated with population change. This leaves but one variable, overwinter survival of juveniles, to explain why populations change in size. Absolute estimates of juvenile survival are available only for Hardwicke Island but a minimum estimate of survival is available for Comox Burn on Vancouver Island where a large area was censused and many of the dispersing grouse were likely found (Zwickel 1983). The minimum estimate of juvenile survival for this stable or slowly increasing population is much higher than that recorded on Hardwicke Island. Thus, high rates of juvenile survival might be associated with population increases and high rates of juvenile mortality might be associated with population declines (unfortunately the "trend" is based on only 2 data points).

The foregoing analysis suggests that none of the demographic variables usually measured for blue grouse populations (with the possible exception of over-winter mortality of juveniles) is consistently correlated with population change. Perhaps this failure to explain population dynamics reflects our inability to measure accurately important demographic parameters or the extreme lack of information on potentially important variables such as dispersal or incidence of non-breeding among yearling females. Another possibility is that there is no universal mechanism of population limitation and that different populations increase, decrease, or remain stable for different reasons. A third alternative is that the causes of population limitation are universal but multifactorial in nature. The latter view need not be untestable or unusually complex and for blue grouse might involve the interaction of 3 demographic variables -- production of young, overwinter survival, and spacing behavior in spring. In any event, the correctness of these speculations can only be tested through experimental manipulations of demographic factors thought to be involved in population limitation and through determination of the biological and environmental reasons that these variables take on the values they do.

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TABLE 9.1. Demographic parameters for populations of blue grouse studied for 3 years or longer.[a]

	Lower Quinsam British Columbia	Middle Quinsam British Columbia	Comox Burn British Columbia	Ash River British Columbia	Sheep River Alberta	Hardwicke Island British Columbia
Population status[b]	stable	stable or slowly decreasing	stable or slowly increasing	increasing	decreasing	decreasing
Survival - adult males	0.69	0.75	0.75	0.66	0.53	0.60
Survival - yearling males	--		0.65	0.60	0.28	0.46
Survival - adult females	0.67	–	0.52 - 0.71[c]	0.53	0.46	0.52
Survival - yearling females	–	–	0.44 - 0.69[c]	0.55	0.48	0.61
Survival - juveniles	–	–	0.41[d]	–	–	0.21 - 0.35
Nesting success[e]	0.75	–	0.57	0.68	≥0.82[f]	0.78
Mean clutch size	6.0	6.3	6.4	6.1	6.2	5.3 - 5.7
Mean brood size	2.4	2.6	2.5	4.0	3.7	2.8

[a] References: Bendell (1955), Bendell and Elliott (1967), Boag (1966), Redfield (1975), Zwickel (1983), Zwickel and Bendell (1967), Zwickel et al. (1983).

[b] Populations ranked from decreasing to increasing in the following order (based on rate of change in numbers of adult males): Sheep River, Hardwicke Island, Middle Quinsam, Lower Quinsam, Comox Burn, Ash River.

[c] Survival of females varied during period of study.

[d] Minimum survival rate based on return of banded juveniles to study areas.

[e] Proportion of clutches in which at least 1 egg hatched.

[f] Only proportion of eggs hatching is presented by Boag (1966), actual nesting success is likely somewhat higher.

TABLE 9.2. Spearman correlations (*r*) between rate of population change[a] and various demographic parameters for populations of blue grouse studied for 3 years or longer.

Parameter	*N*[b]	*r*	*P*
Survival - adult males	6	+0.55	0.13
Survival - yearling males	4	+0.80	0.10
Survival - adult females[c]	5	+0.62	0.13
Survival - adult females[d]	5	+0.70	0.09
Survival - yearling females[c]	4	0.00	0.50
Survival - yearling females[d]	4	+0.40	0.30
Survival - juveniles	2	-	-
Nesting success	5	-0.90	0.02
Clutch size	6	+0.20	0.35
Brood size (August)	6	-0.09	0.44

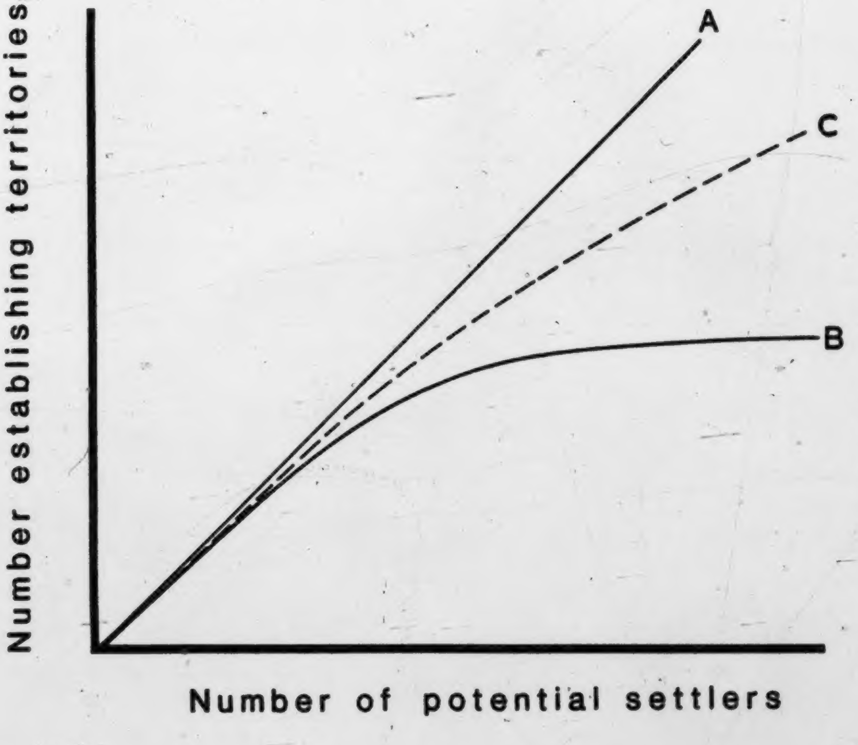
[a] Based on changes in numbers of territorial males.

[b] Number of studies for which data were available.

[c] Based on lower survival rates for Comox Burn (see Table 9.1).

[d] Based on higher survival rates for Comox Burn (see Table 9.1).

FIGURE 9.1. The hypothetical relationship between recruitment and the number of potential recruits when the population is: (A) not limited by behavior, (B) limited by behavior, and (C) influenced both by behavior and the number of potential recruits available (after Davies 1978 and Patterson 1980).


A
C
B
Number establishing territories
Number of potential settlers

10. APPENDIX 1: INFLUENCE OF RADIO PACKAGES ON YOUNG BLUE GROUSE

10.1 Introduction

Radio-tracking frequently is used to obtain information on the behavior and ecology of free-ranging vertebrates but concern has been raised over the potential negative effects of radio-marking on behavior, survival, and reproduction of study animals (Lance and Watson 1979*a* and *b*, Warner and Etter 1983). Some avian species have exhibited excessive feather wear, weight loss, or abnormal behavior when equipped with transmitters (Ramakka 1972, Greenwood and Sargeant 1973, Gilmer et al. 1974, Perry 1981) and, in more extreme instances, spent considerable time attempting to rid themselves of radio packages (Perry 1981).

Studies of the influences of radios on gallinaceous birds have yielded differing results. The short-term effects of radios on galliforms seem well established with most authorities suggesting that after a short period of adjustment birds readily accepted radio packages (Boag 1972, Herzog 1979, Nenno and Healy 1979). In contrast, the long-term effects of radios on reproduction and survival have been judged as either negative (Hessler et al. 1970, Erikstad 1979, Johnson and Berner 1980, Warner and Etter 1983) or inconsequential (Boag 1972, Boag et al. 1973, Dumke and Pils 1973, Lance and Watson 1977). Some of the above results are difficult to interpret because radio-marked and "control" groups often differed in ways other than the presence or absence of radios. Further, because of small sample sizes and various logistical problems, few workers have been able to evaluate long-term effects of radio packages on animals.

As part of a long-term study of the population ecology of blue grouse (***Dendragapus obscurus***), many juvenile grouse were radio-marked in late summer and fall, 1979-1982. The objective of this report is to evaluate the effects that radio-marking had on young blue grouse by comparing the behavior upon release, reproductive success, feather wear, and survival of radio-marked juveniles with similar data for juveniles not equipped with radios.

10.2 Study Area and Methods

Hardwicke Island (77 km^2) is situated between Vancouver Island and the mainland of British Columbia, Canada. Much of the island has been logged and supports a patchwork of successional stages ranging from newly-logged (with only sparse coniferous cover) to mature forest >250 years in age. The main study area for blue grouse research (465 ha) consisted mainly of seral stages <15 years in age.

During late summer and autumn, 1979-1982, 293 juvenile grouse were equipped with radio-packages similar to those described by Brander (1968). Numbers of grouse radio-marked were 60 in 1979, 97 in 1980, 78 in 1981, and 58 in 1982. At time of radio-marking, juvenile grouse were >6 weeks in age and had attained 50-75% of adult weight. All transmitters used in 1979 and 1980 weighed 25 g and all but 9 used in 1981 and 1982 weighed 28 g. The remaining 9 packages weighed 31 g. Packages weighed from 2.1-6.2% of the body weight of juveniles at time of marking ($\bar{X} = 4.10 \pm$ SE 0.05). Radio-marked birds were also marked with color-coded leg bands; other juveniles were color-banded but not equipped with radios. The latter group served as a control with which the performance of the radio-marked cohort was compared. Most radios (93%) were put on large juveniles (males weighing >600 g, females weighing >500 g) after 14 August of each year. To make samples comparable, only large juveniles captured after 14 August were used for the sample of non-radioed grouse

(N = 134). For both groups, daily movements (the distance between the location of an individual on one day and its location on the next day) were measured in late summer. An index of survival was calculated for experimental and control groups from annual return rates (the proportion of juvenile grouse captured one year that were resighted on the study area in the following spring by the census crew). The census was conducted by 2-4 people (each accompanied by a trained pointing dog) who searched the study area on a daily basis from early April to late August. Only radio-marked and non-radioed grouse that were identified by their colored leg-bands were recorded. Thus, the probability of a grouse being resighted was not influenced by the presence or absence of a transmitter. Survival periods (in days), defined as time of capture to time of death, were computed for radio-marked individuals. Fall and winter field work was conducted only during the first 3 years of study. For these years, the relationship of survival to age when marked, body weight, transmitter weight, and ratio of transmitter : body weight was evaluated by stepwise multiple regression (Nie et al. 1975:320).

Further details of general methodology used in studies of blue grouse are given in Zwickel and Bendell (1967) and Zwickel (1982).

10.3 Results

An important assumption underlying the following analyses is that experimental (radio-marked) and control (color-banded only) groups were similar in all regards except for the method of marking. Statistical comparisons of the 2 groups indicated that this assumption was valid as there were no significant differences ($P > 0.05$) in date of hatch, date of capture, age at capture, or weight at capture (Table 10.1).

10.3.1 Behavior Upon Release and Initial Movements

Most grouse were released in dense conifer thickets near the capture site to discourage the birds from flying. On release, 56% of 197 radio-marked grouse walked or ran off, 27% flew strongly, 10% had difficulty in flying and went only a short distance, 3% attempted to fly but could not and instead ran, and 4% remained in the location where released. Non-radioed individuals behaved similarly on release; 56% of 77 individuals walked or ran off, 25% flew away strongly, 13% flew poorly, 3% could not fly and instead ran, and 3% remained where released (contingency $X^2 = 1.08$, 4 df, $P = 0.90$).

Median daily movements during the first 5 days after release were similar for both groups (radio-marked grouse = 0.14 km, $N = 35$; non-radioed grouse = 0.16 km, $N = 78$) indicating that transmitters had minimal effects on mobility (Mann-Whitney U-test, $P = 0.25$).

10.3.2 Survival of Non-radioed and Radio-marked Grouse

No direct comparison of survival rates of non-radioed and radio-marked juveniles could be made as fates of non-radioed animals are more difficult to determine. As indices of survival, proportions of non-radioed and radio-marked grouse sighted by the census crew in the spring following marking were compared (radio-marked grouse known to be present on the study area but not sighted by census crews were treated as "not present"). Return rates of both groups were similar within years and for all years pooled (Table 10.2).

Stepwise multiple regression indicated that the variables age when marked, body weight, transmitter weight, and ratio of transmitter weight to body weight accounted for a significant part (9%) of the variation in survival ($R = 0.30$,

$N = 192$, $P < 0.01$). However, 3 of the correlation coefficients indicated positive influences of radio packages on survival (Table 10.3) and any detrimental influence of these variables appeared to be insignificant.

Although the preceding analyses indicate that radio transmitters had little effect on the overall sample of juveniles, there were 4 known instances of mortality caused directly by harnesses. Three grouse died when harnesses snagged on branches of coniferous trees and another died when its leg was caught in the harness. The only other observed effect of radio packages was feather wear. Fourteen of 18 grouse, recaptured after wearing harnesses for at least 10 months, showed signs of feather wear. Most wear occurred beneath the transmitter package, with lesser degrees of wear near the neck loop and slight amounts near the wing loops. One yearling female died after raising a brood to the age of 7 weeks. Her feathers were very worn beneath the harness and she suffered from a severe case of dermatitis (possibly caused by abrasion from the harness and further complicated by a severe infestation of mites). This dermatitis may have caused the death of the animal (J. A. Hanson, pers. comm.).

10.3.3 Reproductive Success

Fall and winter mortality of juvenile blue grouse on Hardwicke Island was high and, as a result, only a small proportion of the radio-marked grouse survived until spring. Reproductive success of the small sample of radio-marked yearling females was similar to that of yearlings without radios (Table 10.4). Seventy-one percent of the nests of radio-marked yearlings were successful (at least one egg hatched) whereas 87% of the nests of non-radioed yearlings were successful. Clutch sizes and brood sizes at hatching were also similar for both groups.

10.4 Discussion

Negative impacts of radios on birds could be manifested through: (1) behavior, (2) reproduction, and (3) survival. Short-term effects of radios on the behavior of galliforms seem well-documented. Boag (1972) reported that radio-marked red grouse (*Lagopus lagopus scoticus*) were less active and ate less during the first week after capture than did back-tabbed or leg-banded birds. After one week, the differences between radio-marked and non-radioed birds were less distinct. Similarly, Nenno and Healy (1979) found that changes in behavior associated with radio-tagging of wild turkeys (*Meleagris gallopavo*) subsided within 2 days of instrumentation and Herzog (1979) believed that spruce grouse (*Dendragapus canadensis*) readily adjusted to properly-fitted radio packages.

Evidence that radio packages cause lower reproductive rates in galliforms is limited. Radio-marked red grouse established territories and had similar rates of reproductive success to non-radioed individuals (Boag et al. 1973, Lance and Watson 1977). Lance and Watson (1977) reported that radio-marked red grouse discontinued nesting only if they were disturbed early in incubation, which suggested that desertion of nests by radioed birds was likely caused by trauma induced by capture rather than by radios per se. Warner and Etter (1983) implicated heavy radios as a detrimental influence on reproduction of female pheasants (*Phasianus colchicus*). Their data are difficult to interpret, however, because they put heavier transmitters on females during the prenesting period and lighter transmitters on females that were incubating or had already raised broods. Because females of some galliforms are apt to desert nests when disturbed early in the breeding season (Jenkins et al. 1963, Zwickel and Carveth 1978), the results of Warner and Etter (1983) may be an artifact of biased samples rather than a true effect of radio packages. To our knowledge, only Erikstad (1979) has demonstrated adequately a negative effect of transmitters on reproduction. He found that nesting success of banded and radio-marked willow grouse (*Lagopus l. lagopus*) was similar, but that the rate of chick survival was less for radio-marked females than banded hens (possibly because the conspicuously-colored transmitters aided predators in locating broods).

Evidence that transmitters cause increased mortality of galliforms is inconclusive. Radio-marked red grouse survived and established territories as well as did non-radioed birds (Boag et al. 1973, Lance and Watson 1977) and timing of mortality of spruce grouse apparently was not modified by radio-marking (Herzog 1979). Three studies of pheasants suggested that a high ratio of transmitter weight to body weight had a detrimental effect on survival (Hessler et al. 1970, Johnson and Berner 1980, Warner and Etter 1983), whereas another study indicated that radios had little effect (Dumke and Pils 1973). Although Hessler et al. (1970) found high mortality of radioed pheasants, they had no comparable data on non-radioed birds. Thus, it was not certain whether the high rate of mortality that they observed was representative of only radio-marked birds or of all pheasants on the study area.. Johnson and Berner (1980) indicated that pheasants equipped with mock radios survived as well as control animals but also reported a possible relationship between low body weight and low survival of radio-marked birds. Warner and Etter (1983) reported increased mortality associated with high ratios of radio weight to body weight in female pheasants; however, as indicated above, their methodology may have biased the results which might reflect seasonal variation in survival rather than a true influence of radios.

The sample of young blue grouse studied on Hardwicke Island was relatively unaffected by radio-marking. Radio packages weighed 25-31 g or 2.1-6.2% of the body weight of juveniles at time of capture; 49% of the packages exceeded the 4%

maximum recommended by Cochran (1980) with no apparent negative impact. Obviously, at some level, radio weight must eventually become critical in influencing survival but this level could not be determined in the present study. One should note that young blue grouse were still growing and most had only achieved 50-75% of adult weight at time of capture. Thus, the ratio of transmitter : body weight was decreasing rapidly at this time and such estimates may not be equivalent to similar ratios reported for other species.

Although radios had no obvious influence on the total sample of grouse, 4 radio-marked animals died as a direct consequence of the packages and many birds showed signs of feather loss after wearing packages for 10 months or more. Such feather wear might become a more critical mortality factor in areas that are colder than Hardwicke Island.

In summary, radio packages had little measurable effect on behavior upon release, movements, survival, or reproduction of young blue grouse. A review of other studies indicated that there is limited support for the view that reproduction or survival of galliforms is adversely influenced by radio packages. It is uncertain whether the findings for blue grouse on Hardwicke Island can be safely extended to other related species, or even to other populations of blue grouse. There remains an obvious need for studies designed specifically to test the long-term effects of radios on the behavior, reproduction, and survival of wild vertebrates.

10.5 Summary

Effects of radio packages on movements, survival and reproductive success of 293 young blue grouse were studied on Hardwicke Island, British Columbia, during 1979-1983. Similar proportions of radio-marked and non-radioed birds were sighted by census crews in the spring after banding, indicating similar rates of survival in the 2 groups. Survival of radio-marked birds was not influenced by date of hatch, age at capture, date of capture, body weight, transmitter weight, or ratio of transmitter weight to body weight. Radio-marked and non-radioed grouse behaved alike upon release and made similar daily movements during the first 5 days after release. Nesting success, clutch size, and brood size at hatching were similar for radioed and non-radioed females. Harnesses caused deaths of 4 grouse directly and feather wear was observed in 14 of 18 grouse equipped with radio packages for at least 10 months; otherwise, transmitters had little detectable influence on young blue grouse.

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TABLE 10.1. Date of hatch and date, age, and weight when captured for radio-marked and non-radioed juvenile blue grouse, 1979-1982.

Parameter	Radio-marked (*N* = 293)	Non-radioed (*N* = 134)	*P*[a]
Date of hatch	14 June ± 0.4[b]	15 June ± 0.5	0.10
Date of capture	27 Aug ± 0.8	30 Aug ± 1.8	0.46
Age (days)	73.9 ± 0.7	75.5 ± 1.5	0.08
Weight (g)	669 ± 7	670 ± 12	0.40

[a] Mann-Whitney U-test.

[b] Mean ± standard error.

TABLE 10.2. Percentages of radio-marked and non-radioed juvenile blue grouse resighted by census crews on the main study area in the year after marking.

Year of marking	Percent resighted in following year (*N*)			
	Radio-marked	Non-radioed[a]	Total	*P*[b]
1979	13 (60)	11 (72)	12 (132)	0.70
1980	5 (97)	12 (43)	7 (140)	0.17
1981	17 (78)	19 (16)	17 (94)	0.84
1982	9 (58)	33 (3)	10 (61)	--
All years	11 (293)	13 (134)	11 (427)	0.52

[a] To make samples comparable, only large juveniles captured after 14 August were used in the sample of non-radioed grouse.

[b] Probability derived from X^2 contingency tables.

TABLE 10.3. Simple linear correlations between survival (in days after marking) and age when marked, body weight, transmitter weight, and ratio of transmitter weight to body weight for 192 juvenile blue grouse.

Dependent variable	*r*	*P*
Age (days)	+0.13	0.08
Body weight (g)	-0.03	0.73
Transmitter weight (g)	+0.17	0.02
Transmitter : body weight ratio	+0.13	0.08

TABLE 10.4. Nesting success, clutch size, and brood size at hatching for radio-marked and non-radioed yearling female blue grouse.

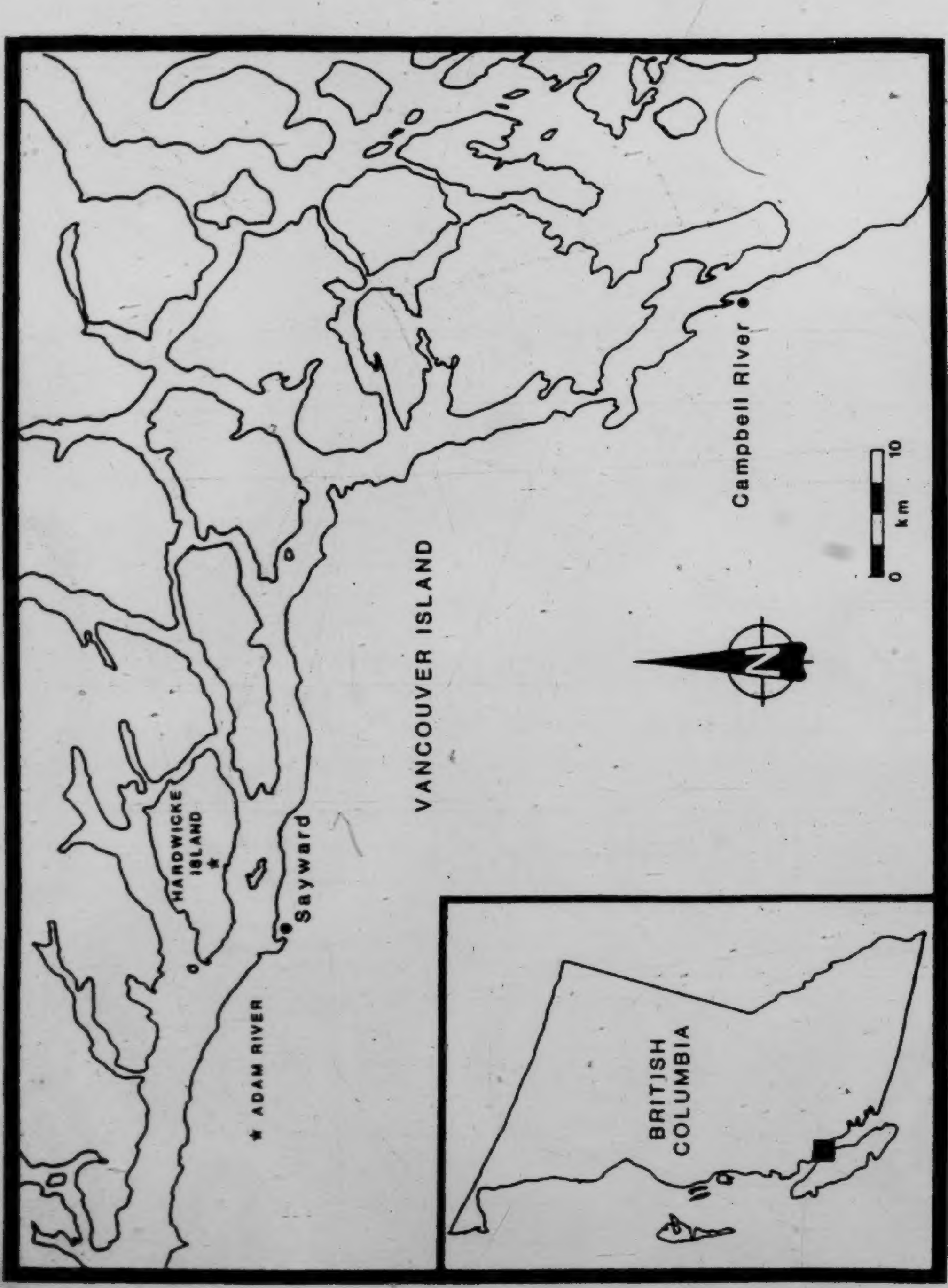
Parameter	Radio-marked	Non-radioed	*P*
Nesting success (%)	71 (21)[a]	87 (15)	0.42[b]
Clutch size ($\bar{X}$ ± SE)	5.0 ± 0.2 (21)	4.9 ± 0.3 (15)	0.43[c]
Brood size at hatching ($\bar{X}$ ± SE)	4.4 ± 0.4 (15)	4.0 ± 0.4 (10)	0.73[c]

[a] Sample size in parentheses.

[b] Fisher's exact test.

[c] Mann-Whitney U-test.

11. APPENDIX 2: THE LOCATION OF THE STUDY SITE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ADAM RIVER
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